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THE ECOLOGICAL DISTRIBUTION OF THE CRANE-FLIES OF NORTHERN FLORIDA

BY

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THE ECOLOGICAL DISTRIBUTION OF THE CRANE-FLIES OF NORTHERN FLORIDA

INTRODUCTION

The extensive group of dipterous insects, known technically as the superfamily Tipuloidea and popularly as the crane-flies, is represented in all parts of the world where moderately moist to humid conditions prevail. Aside from many problems of classification, phylogeny and distribution, the group is of great interest because of the many types of habitats occupied by the immature and adult stages. Here is an old and primitive group of flies[1] with a great number of existing genera and species[2] and often myriads of individuals. Apparently the survival of these flies has been due in part to the fact that they have become adapted to a variety of ecological niches and to many diverse situations that are, so to speak, mere details or by-products of ordinarily recognized animal habitats. Despite the diverse situations that may be occupied by different members of one genus, the immature stages of each species are restricted to a definite habitat; and while the adults of several species are often taken in the same sweep of the net, their larvae will be found to occupy situations that differ in essential details or, if their ecological ranges overlap, to show different limits in their toleration for one or more physical factors.

The study of the crane-flies of northern Florida has involved three more or less distinct problems: (1) determination of the crane-fly population; (2) correlation of each species with one or more of the various recognizable complexes of topography, soil, drainage, and vegetational succession; and (3) explanation of the observed correlation, as far as possible, in terms of the life-history of each species and the requirements of its adult and immature stages.

ACKNOWLEDGMENTS

I am indebted to a number of friends and colleagues at the University of Florida for aid and information: to Mr. Erdman West and Professor M. D. Cody for a number of plant identifications, to Dr. O. C. Bryan for information about the soils of Florida, to Professors T. H. Hubbell and J. R. Watson and to Mr. F. W. Walker for many discussions concerning the animal habitats of northern Florida, and to Professor T. H. Hubbell, Dr. M. D. Leonard and Messieurs Walker, O. C. McBride, D. M. Bates and J. S. Alexander for small but useful collections of specimens from various parts of Florida and the southeastern coastal plain. I wish to express my special

[1] Tillyard (1930) has reported a clearly tipuloid wing from the upper Permian; several tipuloid *genera* and at least one tipulid genus are known from the Mesozoic; and by early Cenozoic the group was apparently as extensive as today.

[2] Not less than 4500 existing species and more than 200 genera are known. Of these, all but 9 genera and somewhat less than 100 species pertain to the family Tipulidae.

gratitude to Mr. F. M. Gaige and the Museum of Zoölogy of the University of Michigan who have made possible much of the field work and the amassing of large collections of adult and immature crane-flies in Florida and other regions; to Professor P. S. Welch for much constructive criticism and many helpful suggestions in the preparation of the present paper; and to Dr. C. P. Alexander of the Massachusetts State College for advice on various taxonomic questions, for checking and adding to my distribution sheets for the non-endemic species that occur in Florida, and particularly for the gift of his large and valuable collection of crane-fly larvae and pupae.

MATERIAL AND METHODS OF STUDY

The specimens upon which this study is based, aside from many adults, larvae, pupae and pupal skins observed in the field but not collected, consist of more than 25,000 adults and approximately 5,000 larvae and pupae. Field work was carried on in 22 of the 28 counties of northern Florida, in 13 scattered counties in southern and central Florida and in 5 counties of the coastal plain of southern Georgia. In addition small collections of adults were made for me in 4 other counties of northern Florida, 5 other counties of southern Florida and from 4 localities in Georgia and Alabama.

In the Gainesville Region, consisting of Alachua County and parts of Bradford, Levy and Marion counties, collections of adults and immature stages were made in all 12 months of various years from 1922 to 1931, inclusive. Field trips into the western portion of northern Florida were as follows: Gadsden County in April; Jackson County in March (twice), April, May and November; Leon and Jefferson counties in February, March and April (twice), May and October; Liberty County in February, March (twice), April (twice), May, July (twice), October and November. Shorter collecting trips were made to most of the other counties of northern Florida in the spring, summer and fall months of various years from 1923 to 1930. Field trips into southern Florida were made in January (Manatee and Sarasota counties); February (Hillboro County); May (Orange and Seminole counties); June (Manatee County); August (Manatee County); October (Dade, Charlotte and Manatee counties) and December (Dade, Manatee and Okeechobee counties).

COLLECTION OF SPECIMENS AND HABITAT DATA

Adult Specimens

The chief method for collecting adults was sweeping and beating the herbage and shrubbery with a net, or flushing specimens from their haunts and netting them in flight. Sweeping was usually preceded by or alternated with a search for resting individuals: these were often collected with forceps or an inverted cyanide bottle from situations inaccessible to the net. One

definite type of habitat was collected from at a time and the specimens were given a field catalog number that referred to a description of this situation. The routine data given in each description included:

1. Exact locality; date; time of day.
2. Topography, drainage, type of soil, plant association.
3. Brief notes on weather (temperature, light, humidity and rainfall) and any present or recent abnormalities of season.
4. Estimates of relative abundance of each species and the proportion of sexes.
5. Cross references to field notes (if any) on the behavior or activities of individual species.

Other methods used to supplement the routine collecting or to obtain special data were lighting, tent trapping and rearing. Many crane-flies are attracted to light and two methods of lighting were employed: (1) On all field trips to distant parts of the state and in interesting seasons in the Gainesville Region a large sheet was hung in a likely situation and lighted with a gasoline lantern. The sheet was watched, usually from slightly after dusk to about midnight and the attracted flies were either netted or taken while they rested on the sheet. (2) In order to obtain as many seasonal records as possible an electrically lighted trap was stationed near the outskirts of Gainesville where it shone over several types of crane-fly haunts. This trap was run once or twice a week throughout the fall, winter and spring months of several years and somewhat less frequently during two summers.

Trap tents, adapted from the original Needham type were used for a part of one spring and gave a number of interesting records, but they were so frequently molested by curious passers-by or domestic animals that they were given up and a plan that might be called "mass-rearing" was adopted. Likely material from the field, such as rotten wood, fungi, small areas of surface soil, mud or leaf-mould, wet sand and silt from stream banks and seepage areas, and mats of liverworts, mosses or algae were placed in large containers, painted black inside (10 gallon tin cans; large stone jars; or tight wooden boxes, 10 x 10 x 10 inches) that opened by way of a hole 1.5 inches in diameter into a mason jar. Each container with its jar was essentially an adaptation of the parasite breeding cage figured by Banks (1909). Several rare and many common species were obtained by this method.

Larvae and Pupae

The collection of larvae and pupae is much slower and more laborious than that of adults. Since the immature stages live in very local situations, concealed in earth, mud, rotten wood, leaf-mould, fungi, mosses, algae mats, silty margins of ponds and streams, on the leaf drift and bottom of brooks, any clue to their whereabouts is worth seeking. The presence of teneral

adults or an abundance of non-teneral adults narrows the search considerably. Empty pupal skins projecting from a log, a patch of moss or soil, although not conspicuous, are more readily found than living larvae and pupae; if fresh, there is a probability that living immatures are close beneath the surface; if old, that the same habitat will be worth searching earlier the next year. Ovipositing females are frequently noted and in nearly all cases the eggs are laid in the future larval habitat. When the larval habitats of several species are known, likely places to search for immatures of related forms are suggested, although here one frequently obtains false clues and meets with numerous disappointments. Finally, a good deal of hit and miss collecting must be done, searching through samples of likely and unlikely material. Even the general rule that the immature stages are confined to damp or wet situations has a few exceptions.

When feasible the immature stages were sought by carefully dissecting away the medium in which their presence was indicated or suspected. This procedure gives much accurate data about the exact habitat and habits and proved the most practical method for taking larvae and pupae that live in rotten wood. For the inhabitants of wet soil, mud and the terrigenous margins and bottoms of streams and ponds this method was rarely practicable and these specimens were best obtained by washing the habitat material through a fine meshed sieve and examining the residue in a pan containing water. When algal mats, mosses, or liverworts formed the habitat, the material was washed free of silt and then carefully shredded in a white pan containing water. The larvae that live in the thin diatomaceous sludge of dripping cliffs and rocks were usually hard to find during the day but were frequently found creeping over the surface of the wet rocks at night.

All collections of larvae and pupae were accompanied by field catalog records and, as in the case of adults, the specimens taken from one situation on the same date were given the same catalog number. The data secured varied with differences in the type of habitat but in all cases the following items were recorded:

1. Exact locality; date; time of day.
2. General type of habitat; topography; drainage; vegetational association.
3. Precise part of general habitat; stratum; local details.
4. Other animals present.
5. Cross reference to field notes on special habits of individual species.

Field Observations

A considerable portion of the field work was devoted to observing the behavior of both adult and immature stages in their natural haunts. Whenever an opportunity occurred to observe activities, attention was directed to

securing notes rather than to collecting; or, at any rate, to making observations and notes before collecting. The most fruitful times for observation in the field were cloudy days, twilight and night. A comparatively few species are most active in the moderate light of open hammocks during daylight hours and spend the night resting on or beneath the leaves of the herb and lower tree strata. The majority of the species rest quietly during the day and only become active when the light is reduced and the humidity increases. At these times the feeding, mating, ovipositing of adults and, more rarely, the behavior and feeding habits of larvae were observed. An electric or acetylene headlight with a moderately bright beam gave the best results for night observation and despite the adults' usual positive response to artificial light, when feeding, mating or ovipositing, they were rarely disturbed by the headlight. Most of the larvae were more sensitive and retreated from the surface of the algae, wet rock, or liverworts where they were feeding unless the light was greatly reduced.

Rearing of Immature Stages

In order to make positive identification of the larvae and pupae taken in the field it was necessary to rear representatives of each species and when possible each species was reared several times, both as a check against error and to ascertain additional details of the life-history. The rearing cages were shell vials, jelly glasses or glass jars and the conditions of the natural habitat were simulated as closely as possible.

Five of the species that were reared began the life cycle as fertile females, taken while ovipositing in the field; and the adults of nearly a score of the species that were reared from larvae, mated and oviposited in the cages. From these, eggs and younger larvae, difficult to find in the field, were obtained. Altogether more than 2,000 adults representing 74 of the 128 species known to occur in northern Florida emerged in the breeding cages. Of these, 47 were reared twice or oftener.

Usually, non-lotic larvae, that feed upon plant tissues, or are scavengers, were not difficult to rear. Predacious larvae are nearly always voracious and often cannibalistic so that individual breeding cages were required for each larva and living food (small oligochaete worms or small herbivorous crane-fly larvae) added at frequent intervals. The species from lotic situations were successfully reared in wet mosses but usually died when an attempt was made to simulate the natural habitat. Nearly all pupae could be reared by placing them in damp mosses or within loose folds of damp filter paper.

Various devices were used to prevent the larvae and pupae from concealing themselves within the habitat medium. In the case of inhabitants of moss, liverwort or algae a few shreds of the plant placed on wet filter paper in a petri dish enabled one to keep a specimen under observation for several days

or, if fresh material was frequently provided, for a number of weeks. The inhabitants of earth, mud and rotten wood were placed between two narrowly separated sheets of glass (lantern slide covers) that contained a layer of fine material from the habitat. If these narrow glass cages were kept in opaque petri-dishes on a layer of wet filter paper the confined larvae could be carried through to pupation and emergence. In some cases, when an abundance of specimens permitted, 12 to 30 rearing jars were started; then every few days one of the jars was examined and discarded.

Laboratory Observations on Living Specimens

The activities of larvae and pupae were watched with the naked eye, with a hand lens or as high powers of the binocular as did not necessitate great illumination. Notes on colors, methods of locomotion, reactions to light, moisture and contact were made and hatching, ecdysis, feeding, tube-construction, pupation and emergence of various species were observed. Nearly all of the work was done in an unheated building and advantage was taken of this circumstance to note the effect of temperature on the activities of the immature stages. For a number of species observations were made on the effect of slowly dessicating the contents of breeding jars and on the reactions of larvae to gradients of moisture content in soil or rotten wood.

The adults obtained in the breeding cages provided many opportunities to observe details of various activities. Mating and ovipositing were watched with a lens or Zeiss stereo-magnifier. Oviposition was usually made in selected spots in the material from which the adult had emerged, but females of numerous species when placed in a jar containing only moist filter paper would oviposit in the latter where the eggs could be found and counted. In a few cases when mating did not take place naturally it was possible to obtain fertile eggs by holding the male and female by the wings with the forceps and bringing their bodies into contact; whereupon the male would seize the female in his copulatory apparatus and complete the process. Reared adults of a number of species were utilized for simple experiments on reactions to light, humidity, evaporation rate, and temperature, and to determine the survival time in air of various percentages of humidity.

NORTHERN FLORIDA AS A FAUNAL AREA

Northern Florida, as arbitrarily limited in the present paper, extends south from the Georgia line to include Levy, Marion and the northern part of Volusia counties, and west from the Atlantic Coast through the tier of counties along the west side of the Apalachicola River. This area lies within Fenneman's Coastal Plain Province of the Atlantic Plain (Fenneman, 1928) and includes the junction of the Sea Island, Floridian and East Gulf Coastal Plain sections.

In spite of its low altitude and the monotony of coastal plain topography, northern Florida displays many minor variations of relief and a diverse and irregularly distributed series of plant and animal habitats. In the northwestern part of this area (East Gulf Coastal Plain) a narrow low upland has been deeply dissected; slightly west of the central axis of the peninsular portion there is a slight ridge of low, rolling hills; elsewhere the surface drainage is in a youthful stage with numerous lakes and extensive marshes, swamps and flat-woods, with little or no development of master streams. The soil of practically the whole region is either residual or derived from unconsolidated marine sands, and the many types and varieties have an extremely irregular distribution. Over most of this area the water table shows marked and often very local variations in level, due largely to extensive development of a Karst topography with numerous sink holes, sink-hole ponds and lakes, and a tremendous volume of underground drainage.

The abrupt changes in soil, drainage and depth of the water table are usually marked by equally abrupt changes in the vegetation, although in numerous cases, due to the small relief and perhaps associated with both vegetational succession and wide seasonal variation in rainfall and water table, there is an extensive intergrading of several vegetational types.

CLIMATE

Temperature and Precipitation

Outstanding features of the climate of northern Florida are the mild comparatively dry winters and the long summers with a pronounced midsummer rainy season. This seasonal contrast in rainfall is more marked as one goes farther south into the peninsular portion of the state, but is quite distinct throughout all of northern Florida except the western portion. There, although the annual rainfall is approximately equal to that of the peninsular region, it is more evenly distributed throughout the year.

This seasonal variation in rainfall is conspicuously reflected in seasonal changes of water level in the numerous swamps, marshes and bodies of open shallow water, and in the change of extensive flat-wood formations from dry, parched, easily-burned-over areas to wide extents of marshy or shallowly inundated lands. Another noteworthy feature of the rainfall is its irregular variation over a period of years. At Gainesville the Weather Bureau records show a mean annual precipitation of 49.11 inches for the period 1900-1926, but the annual rainfall for 1911 was 38.84 inches; 1912, 61.04 inches; 1917, 32.79 inches; 1920, 63.71 inches; 1923, 41.72 inches; and 1924, 61.96 inches. This irregular fluctuation, most marked for the comparatively dry months of winter and spring, is also associated with pronounced fluctuations in the water-table and the drying up or abnormal flooding of shallow water basins.

Probably the most important feature of the yearly temperature is the

mildness of winter. Not only are minimum temperatures relatively high, but they are of short duration. Rarely are temperatures of 32°F. or lower experienced on more than two or three successive days and more rarely still will a temperature as low as 32°F. be maintained throughout 24 hours. During these ordinarily brief periods of freezing temperature, many local spots, sheltered by proximity to water, by the evergreen hammocks, or by areas of heat-retaining soil, escape the frost.

Figure 2 and Tables I, II, and III, reproduced or excerpted from "The Climate of Florida" (Mitchell and Ensign, 1928) show the average monthly rainfall and the monthly maxima and minima of temperatures, as well as extremes of drouth and low temperatures for several stations in northern Florida.

TABLE I. *Mean maximum and minimum monthly temperatures, in degrees Fahrenheit, at various stations in northern Florida, 1910-1926.*

	Cedar Keys Levy County		Gainesville Alachua County		Marianna Jackson County		Tallahassee Leon County	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
January	67.2	50.2	68.5	47.1	65.1	41.1	63.6	44.5
February	67.2	50.6	69.8	47.0	66.7	42.3	65.3	45.2
March	72.3	56.1	75.5	51.9	73.3	47.7	71.9	51.4
April	78.0	62.1	81.3	57.3	80.5	53.7	78.7	56.5
May	83.9	68.5	86.6	63.3	86.8	61.5	84.9	63.5
June	88.2	74.0	89.7	68.8	91.9	68.4	89.5	69.8
July	89.0	75.4	90.1	70.7	91.5	70.4	89.0	71.3
August	89.7	75.5	90.7	70.9	91.9	70.4	89.4	71.5
September	88.8	73.3	88.9	69.0	89.9	67.2	87.0	69.0
October	82.9	66.0	82.7	62.0	81.8	57.5	79.0	60.9
November	73.9	55.6	74.0	50.9	72.0	45.0	69.7	49.4
December	67.2	50.8	68.9	47.4	66.1	42.1	63.9	45.4

Relative Humidity and Evaporation Rate

Relative humidity, as one of the chief factors in determining evaporation rate, is of great importance in the habitat distribution of crane-flies; but published records for relative humidity are limited to readings made at a few coastal Weather Bureau Stations at fixed intervals of the day—7 a.m., 12 noon and 7 p.m.—and are available only as monthly means. Published records pertaining to northern Florida are given in Table IV.

Inland, the percentage of relative humidity, when taken at all seasons and hours, and in all types of habitats, shows extremes of 20 to 100%. In the drier spring and fall months the relative humidity, just above the herb stratum, may fall to 30 or 35% in mid-afternoon, even within extensive mesophytic hammocks, while nights with percentages of 85 to 100% are frequent in even the driest habitats. In the winter months low relative humidities are less frequent and extreme, and during the rainy season the diurnal percentages within shaded habitats, usually range from 70 to 90%.

TABLE II. *Miscellaneous prolonged dry periods recorded at weather bureau stations of northern Florida.*

Station	Year	Duration	Number of days	Amount of rain, inches
Pensacola.........	1891	Sept. 14 — Nov. 20	68	0.54
"	1892	Mar. 27 — June 15	81	1.00
"	1898	Apr. 20 — June 13	55	0.25
"	1906	Oct. 6 — Dec. 15	71	0.88
"	1911	Jan. 3 — Mar. 21	78	0.49
"	1914	May 6 — June 8	36	0.00
"	1925	Sept. 14 — Sept. 25	14	0.00
Jacksonville.......	1871-2	Dec. 15 — Jan. 18	35	0.00
"	1875-6	Dec. 12 — Jan. 5	25	0.00
"	1883	Oct. 24 — Nov. 18	26	0.00
"	1883	Nov. 21 — Dec. 24	34	0.00
"	1889	May 2 — May 28	27	0.00
"	1889	Sept. 25 — Oct. 31	37	1.26
"	1889	Nov. 1 — Dec. 31	61	0.51
"	1890	Jan. 1 — Jan. 31	31	0.63
"	1890	Feb. 1 — Feb. 28	28	0.51
"	1892	Mar. 13 — Apr. 7	25	0.00
"	1895	Sept. 16 — Oct. 14	29	0.00
"	1906-7	Nov. 1 — Mar. 31	151	2.55
"	1908-9	Nov. 1 — Jan. 31	92	2.54
"	1910-11	Nov. 1 — Feb. 28	120	3.73
"	1916	Jan. 1 — Apr. 30	121	2.14
"	1917	Jan. 1 — May 31	151	6.34
"	1917	Oct. 1 — Nov. 30	61	0.61
"	1922	Nov. 2 — Dec. 9	38	0.00
"	1925	Apr. 11 — May 13	33	0.00

Differences of evaporation rate between the various major habitats are marked. Figures 3 and 4 show the comparative evaporation rates for several types of major habitats in the Gainesville Region. In both instances the measurements were obtained with pairs of Livingstone standard spherical atmometers, restandardized monthly and rain-proofed in the manner described by Livingstone (1915) and Thone (1924). Each pair consisted of a white and black bulb. The former gave a measurement of the standard evaporation rate, the latter of the increase in rate due to direct insolation. The figures show mean daily evaporation rates in milliliters for the weekly intervals given. Figure 3 is for evaporation rates 20 centimeters above ground for 6 contrasting types of northern Florida habitats from March 1, 1929 to July 15, 1929. Figure 4 is one published by Dr. Frank Thone (1927) for evaporation rates in hammock and ravine at Gainesville, October 15, 1924 to May 3, 1925.

Natural Habitats of Northern Florida

A number of more or less tentative subdivisions and classifications of the various complexes of vegetation, topography, soil and drainage found in Florida have been proposed. Harper in a number of publications (1910, 1914, 1921) has subdivided the state into a rather large number of areas that

TABLE III. *Number of days with minimum temperatures of 32, 25, 20, 16°F., or below, recorded at various stations in northern Florida.*

°F	Cedar Keys Levy County				Gainesville Alachua County				Marianna Jackson County				Tallahassee Leon County			
	32	25	20	16	32	25	20	16	32	25	20	16	32	25	20	16
1889–1900...					13	6	1	0					17	7	2	0
1900–1901...					10	2	0	0	20	4	0	0	14	2	0	0
1901–1902...					20	5	1	0	41	11	4	1	20	6	2	0
1902–1903...					9	2	0	0	15	7	1	0	6	3	0	0
1903–1904...					16	1	0	0					18	2	0	0
1904–1905...					19	4	2	1	35	18	6	3	17	5	2	0
1905–1906...					2	0	0	0	19	0	0	0	10	00	0	0
1906–1907...					8	3	1	0	13	2	0	0	8	2	0	0
1907–1908...	0	0	0	0	10	0	0	0					10	1	0	0
1908–1909...	2	0	0	0	5	2	0	0	12	5	2	0	3	2	0	0
1909–1910...	0	0	0	0	12	3	2	0					21	2	2	0
1910–1911...	2	0	0	0	11	1	0	0	24	5	2	0	15	3	0	0
1911–1912...	4	0	0	0	17	2	0	0	34	6	0	0	18	4	0	0
1912–1913...	0	0	0	0	3	0	0	0	25	1	0	0	2	0	0	0
1913–1914...	0	0	0	0	10	0	0	0	35	1	0	0	11	0	0	0
1914–1915...	1	0	0	0	8	1	0	0	20	4	0	0	12	1	0	0
1915–1916...	3	0	0	0	18	1	0	0	25	5	0	0	10	0	0	0
1916–1917...	8	1	0	0	14	3	2	0	27	12	4	1	15	5	2	1
1917–1918...	16	2	1	0	21	11	2	0	41	20	6	3	25	10	4	0
1918–1919...	4	1	0	0	9	3	0	0	21	4	2	0	11	3	2	0
1919–1920...	2	0	0	0	18	1	0	0	21	7	0	0	18	2	0	0
1920–1921...	0	0	0	0	1	00	0	0	15	0	0	0	3	0	0	0
1921–1922...	2	0	0	0	5	0	0	0	17	3	0	0	8	0	0	0
1922–1923...	1	0	0	0	7	1	0	0	12	1	0	0	4	1	0	0
1923–1924...	4	1	0	0	12	2	0	0	28	5	2	2	12	4	2	1
1924–1925...	0	0	0	0	4	0	0	0	11	00	0	0	5	0	0	0
1925–1926...	3	0	0	0	11	4	0	0	21	5	1	0	16	3	1	0
1926–1927...	7	1	0	0	11	3	1	0	15	5	2	1	12	4	1	1

TABLE IV. *Monthly means, percentages of relative humidity at three northern Florida coastal weather bureau stations.*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Apalachicola													
7 A.M.	86	85	82	83	80	82	83	84	87	84	82	88	84
12 N.	71	68	65	66	64	69	68	70	70	65	62	75	68
7 P.M.	79	78	75	77	74	79	78	78	79	75	74	83	77
Jacksonville													
7 A.M.	86	84	83	79	79	81	83	85	86	84	85	86	83
7 P.M.	77	74	71	69	72	77	78	81	82	79	77	77	76
Pensacola													
7 A.M.	82	80	81	79	77	79	82	83	82	77	78	82	80
7 P.M.	78	76	76	74	72	75	78	77	74	68	71	75	75

show more or less distinct and characteristic plant associations and has recently simplified and summarized this work in a vegetational and soil map of the state (Harper, 1925) which is reproduced, in part, as Figure 5. After extensive field work over most of Florida, particularly the northern part, I believe that this map gives a good generalization of the distribution of the

predominant types of vegetation and topography, but as Harper himself has stated, "Nearly every area mapped as one type shows streaks or patches of most of the others." Watson (1928) has given a useful discussion of the main types of Florida habitats and Byers (1930) has discussed the "biotic areas" with special reference to the dragonflies. The Wrights (1932) have given a detailed description of Okefinokee Swamp which extends slightly into Florida near the eastern end of the Georgia-Florida line and contains a number of types of habitats that are well represented in northern Florida. Many of the excellent photographs in their paper appear typical of certain extensive or frequent formations to be described below, particularly swamps "prairies," lower streams and pine flatwoods.

In the present paper 19 typical and more or less frequent features or complexes of topography, drainage, soil, and vegetation, or "major habitats," have been recognized for northern Florida. The characterization and classification of these was begun in the Gainesville Region, in the peninsular or southeastern portion of northern Florida, and probably apply best to this area. The descriptions have been extended and modified, however, from extensive field notes for all localities where collecting has been done and checked against observations made along most of the main roads and many side roads of the whole area.

Sea Coast Habitats

1. *Juncus Flats of Tidal Marshes.*

The only habitats conditioned by marine association in which any Florida crane-fly has been found to breed, are the extensive Juncus marshes of the shallow tidal flats and estuaries. The best development of these formations, which are practically pure and usually dense stands of *Juncus roemerianus,* growing to a height of 3-6 feet, is found on flats that are inundated for several hours at high tide by very brackish or almost pure sea water and exposed for somewhat longer periods at low tide. The Juncus formations are usually bordered or dotted with dense fringes or islands of black mangrove, *Avicennia nitida,* and are thickly populated with fiddler crabs and burrowing polycheate worms, resembling Nereis. Here in the thin, tenacious mats of algae on the lower stems of Juncus and on the soil between the plants is the habitat of the immature stages of *Limonia floridana,* and myriads of adults may be found at certain seasons flying, mating and resting among the erect spikes.

Inland Habitats

AQUATIC AND SEMI-AQUATIC SITUATIONS

A. Streams

2. *Seepage Areas and Small Rills.*

Seepage areas are helocrene springs whose cool waters percolate through the surface soil and produce small to moderate sized areas of saturated, often

boggy earth. In some cases such areas form the origins of small rills but in many cases they are isolated patches of saturated earth, in which the soil-water has more or less flow. Although usually small and inconspicuous, sometimes with an extent of but a few square yards, they are a common feature of nearly every small stream valley and occur on the sides of a number of the larger sink-holes. These seepage areas and the rills derived from them, or from rheocrene springs, are usually associated with and shaded by hammock vegetation, and the boggy earth usually contains wood fragments in an advanced stage of decay, often covered with luxuriant patches of mosses and liverworts. In most instances the water is circum-neutral or but slightly basic (pH 6.6-7.6) but on some of the deeper slopes the seepage from rapidly disintegrating limestone strata has a pH of 8.5. Both types have a characteristic and often abundant crane-fly fauna.

3. *Small Streams.*

Most of the brooks and small creeks of northern Florida have bottoms of rolling sand with very few gravel riffles and little development of deep, quiet pools. Clumps of leaf drift are frequent and, aside from the sandy bottom and an occasional log or root, offer the main lodging places for thigmotactic animals. The margins usually include stretches of saturated silt (in most cases on top of wet, packed sand), wet sand and steep or vertical banks of deep rich soil, often covered with deep mats of mosses and liverworts.

The water derived from springs or diffuse seepage areas is clear and colorless and varies from circum-neutral to slightly basic, but the surface drainage and the seepage from swamps and flatwoods are colored a distinct brownish tinge and are more or less acid (pH 5.5-6.2). Most streams at some distance below their heads contain a mixture of these two kinds of water that varies with the locality and season, but a number of streams have clear and circum-neutral water throughout the year. Most of these streams are shaded by hammock vegetation and, except near the coast, lie in narrow valleys that support a well-developed hammock vegetation and are the sites of frequent seepage areas.

4. *Swamp and Bog Streams.*

Streams that originate in, or flow through areas of, swamp or swampy hammock are often greatly modified in character and fauna. When the swampy area is extensive, low-lying, and level, the streams develop a characteristic lagoon-like appearance. Their sluggish currents of strongly stained, acid water flow over deposits of semi-suspended silt between low, indefinite banks. Where deeply shaded, such streams are bordered by bare swamp floors with frequent cypress knees and sodden, moss-covered logs; where the shade is less complete or constant, rank growths of lizard's-tail *(Saururus*

cernuus) and other herbage conceal the shore line and choke the shallower channels.

Some of the rills and brooks that traverse the small swamps of sloping valley bottoms, develop bog conditions. Usually, in such cases, the streams break into wandering channels between root-bound platforms of hardwood trees, and the numerous ponded areas and secondary courses are filled with dense growths of sphagnum and show a typical sphagnum bog acidity, (pH 4.0-5.0).

5. *Larger, Calcareous Streams.*

A number of creeks and small rivers of northern Florida derive their water from huge springs or from clear lakes of calcareous water. Such streams flow over clean-swept beds of strongly pitted limestone and residual gravel and boulders. Their clear water often has rank growths of submerged aquatic plants, *Sagittaria natans, Elodea* sp, and *Vallisneria spiralis* (eel-grass), while thick coats of coarse mosses grow on the submerged surface of constantly wet rocks. These mossy rocks have a considerable lotic fauna, including crane-fly larvae of 3 species, *Corydalis cornuta,* several species of mayfly and dragonfly nymphs, and caddis-fly larvae. The rooted, submerged aquatic plants have a large population of the snails, *Goniobasis catenaria* and *Viviparus wareanus,* which, in northern Florida, appear to be restricted to these calcareous streams.

6. *Lower Streams.*

In nearly all of the lower streams, the water is derived in large part from swamp and flatwood seepage, often by way of lakes, swamps, and marshes. These streams are usually subject to great fluctuations in volume, due both to the seasonal differences in rainfall and to variations in the amount of water they may lose to subterranean drainage systems. Often their flood-plains have bayous and extensive areas of well-developed swamps. Except for the Apalachicola River, which derives most of its water from the red clay lands of Georgia and Alabama, the streams of Florida carry little silt save light, flocculent clots of colloidal iron and humus which, together with the brownish tinge of the water, gives most of the lower streams a dark or black appearance with reflected light.

B. Ponds, Lakes, Marshes and Swamps

These are all common and typical features of the topography of several extensive areas of northern Florida and at least a few examples occur in most of the counties of the state. Nearly all owe their formation to the solution of limestone strata, but in spite of a similar origin they show a great range of variation. Differences in the original thickness of the dissolved limestone, in the extent of the solution areas, in the depth and nature of the strata that

lay above the limestone, and in age, together with marked local and individual differences in water supply and drainage, have contributed to this diversity. All gradations exist between the types described, although these are represented by numerous examples. Most of the ponds are apparently not successional stages of former lakes but the sites of originally small solution cavities. Some of the ponds of the rolling, sandy lake country are probably the remains of small lakes, but for most of the shallow lakes the succession appears to be directly into extensive marshes.

7. *Fluctuating Ponds.*

Many ponds have been formed by a local solution of thinly buried shallow limestone strata and their basins are very shallow with gently sloping sides that have no definite boundaries. Their water shows great seasonal fluctuations in area. Near the end of the rainy season, when they reach their maximum extent, they may be several times larger than at the end of the dry season, and occasional years of abnormal rainfall or drouth cause even wider variations. These periodic and sporadic fluctuations prevent the development of any permanent vegetation within the broad zone of fluctuation. As the water recedes in the dry season, it leaves a belt of saturated earth in which some grasses and sedges spring up among mats of stranded algae and other aquatic vegetation. As the dry season progresses the outer portion of this zone becomes quite dry but there usually remains an inner margin of saturated, dark muck soil. The permanent water is usually filled with submerged, floating, and emergent aquatic plants and may support extensive floating mats of green algae. Such ponds have a rich invertebrate and vertebrate fauna.

Some of the smaller fluctuating ponds are surrounded by low hammock formations. Here herbaceous vegetation is largely absent and receding water leaves a broad zone of bare, black muck that remains wet throughout the great part of a normal dry season.

8. *Sink-Hole Ponds.*

Sink-hole ponds are due to the solution of comparatively thick, deep-lying, limestone strata. Usually less than an acre in extent, their banks are steep both above and below the water line, which is approximately that of the local water table. The relatively slight seasonal fluctuation in level results in but small changes in areas and well-marked, narrow zones of permanently wet earth, emergent and floating vegetation are well established. The water is comparatively deep, 12-20 feet, clear and slightly basic. Included in the rich invertebrate fauna are nearly always large numbers of green hydra and huge numbers of planarians.

9. *Lakes.*

The lakes of the different regions of northern Florida fall into several more or less distinct types. Generally speaking, those of the sand regions

were formed by the solution of limestones at a considerable depth beneath the surface of the water. They occupy many of the deeper depressions of rolling, pine and scrub-grown country and are usually characterized by clear, colorless, spring-fed water that is circum-neutral or somewhat basic, and by clean sandy bottoms and shore lines. They show but little fluctuation in water level and the pine and scrub vegetation of the sand hills grows down close to their margins. These are the deepest of the Florida lakes and usually have the largest proportion of open water, although zones of rooted, aquatic vegetation are developed along the more sheltered shore lines. Some of these lakes, however, show a considerable development of marsh conditions.

The lakes of the hammock and flatwoods areas are generally more shallow, and their surfaces are not much lower than that of the surrounding country. Many of them have been produced by repeated sink-hole formation along the course of a former surface stream. (Sellards, 1914). Such lakes are subject to distinct seasonal fluctuations and to even more marked occasional fluctuations caused by years of abnormal rainfall or the vagaries of their subterranean drainage. In most instances, their water, derived from surface run-off and shallow seepage, is moderately or strongly colored and ranges from circum-neutral to slightly acid. The sandy bottoms of these lakes are covered with a deposit of fine, organic silt that may be from an inch to more than a foot in depth and foot prints and other shallow depressions along their low beaches accumulate a thin stratum of soft, saturated silt. These lakes show great variations in their aquatic vegetation; in many, the succession is directly toward swamp conditions with extensive development of cypress along the muddy shores; in others there is a distinct development and zonation of marsh vegetation before the shallow water is invaded by cypress or hardwood swamps. Intermediate types of lakes occur in parts of the hammock regions. These are apparently similar to the lakes of the sand region in origin and depth but derive much of their water supply from surface run-off and from swamps that form a part of their shore line.

10. *Marshes.*

Numerous ponds and lakes have become almost or completely converted into marshes and many others show considerable development of marsh vegetation. Where the shorelines are not subjected to large fluctuations in water level or frequent wave action, distinct zones of herbaceous plants are developed. Where zone-formation is most complete, the inner, deeper zone consists of *Nymphaea macrophylla* (yellow water lily, "bonnets"), and *Castalia odorata* (white water lily). These grow in water that is usually 5-8 feet deep. Shoreward, in increasingly shallower water, come successively zones of *Panicum hemitomon* (maiden cane), *Sagittaria lancifolia* (arrow head), *Pontederia cordata* (wampee) and either *Typha latifolia* (cat tail), *Scirpus* sp. (bull rush), *Cladium effusum* (saw grass) or else a mixture of some of

these with other herbaceous plants. The extent of each zone depends, among other factors, upon the amount of wave action, the slope of the bottom, and the fluctuations of the water level, but one can find numerous instances where any one of these zones is many yards in width.

In numerous broad, shallow lakes of the hammock and flatwoods areas the typical plants of the outer margin are absent because of the pronounced seasonal fluctuations of the water line, while the great expanses of open water are filled with dense growths of Nymphaea, Castalia and the completely submerged Ceratophyllum and Vallisneria. In most of these lakes and in many others where rooted aquatics are but little developed, the water hyacinth, *Piaropus crassipes*, introduced into Florida about 1890, comprises the dominant vegetation and forms huge floating rafts and mats that tend to conceal or choke out other vegetation and rapidly produce great quantities of fine peat and organic debris.

The later stages of marsh succession are greatly varied by local conditions. Occasional pure stands of cat tails or bull rushes occur but marshes of coarse, tall grasses and sedges, mixed with Pontederia, Sagittaria, and other herbage and often dotted with such bushy shrubs as button bush *(Cephalanthus occidentalis)*, hurrah bush *(Pieris nitida)*, and *Decodon verticillatus*, are far more common and extensive.

11. *Swamps.*

Swamps are another common and conspicuous feature of many parts of northern Florida and they also show many diversities of size and composition. Many of them are due to succession in solution depressions; others have been developed along the flood plains and estuaries of both large and small streams.

"Cypress Ponds": These occupy shallow depressions that are abundant in and typical of all flatwoods regions. They are usually more or less circular and vary in size from an acre to perhaps 50-75 acres. In the rainy season their water may have a depth of several feet, and in the dry season it may entirely disappear or, at most, be restricted to a shallow pool in the center. The dominant tree is the pond cypress *(Taxodium imbricarium)* but the slash pine *(Pinus caribaea)*, black gum *(Nyssa biflora)*, red maple *(Acer rubrum)*, white bay *(Magnolia virginianum)*, red bay *(Persea borbonia)*, and guinea cypress *(Hypericum fasciculatum)* are well represented. About the margins there is usually a thick growth of shrubs and small trees, including several species of Ericaceae and Ilex, tangles of Smilax, and frequent patches or hammocks of Saururus, sedges, grasses, and ferns. In the dry season, the floor of the interior includes areas of bare mud and peat, strewn with moss-grown logs in all stages of decay. Luxuriant patches of sphagnum often occur about the logs and cypress knees.

"Bays": Related to the cypress ponds and integrating with them is a type of dense, acid swamp, known in Florida as a "bay." These are de-

veloped in depressions that show less fluctuation of water level than do those occupied by cypress ponds. They may contain some cypress but have a much higher proportion of hardwood trees and shrubs, forming dense thicket-like growths that are difficult to penetrate. The bays usually show some development of sphagnum and frequently include small areas of typical sphagnum bog.

Swamps Associated with Streams and Lakes: About many lakes, particularly those of the hammock and flatwoods regions, and along the courses of both small and large streams, there are frequent developments of swamp conditions. These swamps vary from small patches and narrow zones to large extents of uniform swamp conditions and range from almost pure or preponderant growths of cypress to hardwood swamps. The latter may be almost pure stands of black gum or mixtures of black gum, red maple, white bay, red bay, sweet gum and ash. The composition of the swamps appears to be associated to a considerable extent with the fluctuation of the water level, cypress being found where the seasonal fluctuation is more extensive, but the cutting-off of the cypress has, no doubt, tremendously altered the character of many former cypress swamps. The hardwood swamps have shorter periods of high water and are much wetter in the dry season, their soil being nearly always saturated. The larger hardwood trees often have small, root-bound platforms about their bases that are perhaps a foot above the general level of the swamp and between these platforms are irregular channels and depressions where shallow water, saturated silt and small accumulations of peat occur. Both the cypress and hardwood swamps contain an abundance of wet, rotting wood, often overgrown with thick coats of mosses or mosses and liverworts. Grasses, sedges and extensive patches of Saururus occur in the more open areas and luxuriant clumps of ferns grow from small hummocks and well-rotted logs of both the open and deeply shaded portions.

TERRESTRIAL SITUATIONS

A. Hammocks or Hardwood Formations

In northern Florida, the term hammock is applied to all hardwood formations except swamps and the dry "scrubs" and turkey oak second-growths. As so limited, hammocks range from low hammocks which intergrade with swamps to high hammocks characterized by well-drained or dry sandy soils and a rather open growth of trees, among which either the live oak *(Quercus virginiana)* or the red oak *(Quercus falcata)* and post oak *(Quercus stellata)* are usually conspicuous. Intermediate between these extremes, and probably forming the climax association of northern Peninsular Florida, is the Magnolia-Laurel Oak-Holly-White Oak Hammock.

12. *Low Hammock.*

The low hammocks differ from hardwood swamps in having a water table that is below the surface of the soil. They contain many plants characteristic of hardwood swamps and probably, in most cases, represent a stage in succession from swamps. The sweet gum is perhaps the most characteristic tree but black gums and an occasional cypress may occur. Red maple, white bay, hackberry (Celtis), water oak *(Quercus nigra)*, hornbeam (Carpinus), tulip poplar (Liriodendron) and slash pine are usually represented. The soil is often saturated for considerable periods and even in the dry season remains moist and wet; all fallen wood becomes water-logged and passes into stages of wet decay, often associated with luxuriant growths of moss, and the leaf mould becomes sodden and matted into the damp silty soil. Much of the floor is bare of herbs but some of the swamp undergrowth persists until it is slowly replaced by the characteristic undergrowth of the Magnolia hammocks.

13. *Magnolia-Laurel Oak-Holly-White Oak Hammock.*

The most characteristic tree of the climax hammock is the magnolia *(Magnolia grandiflora)*. It is absent or rare in the low and in the driest hammocks but is probably the most common large tree of mesophytic formations. Commonly associated with the magnolia and forming a considerable element of the magnolia hammocks are *Hicoria glabra*, *Quercus laurifolia*, *Carpinus caroliniana*, *Pinus glabra*, *Quercus alba*, and *Ilex opaca*. Where the hammocks are developed upon richer, calcareous soils, *Sabal Palmetto* forms a conspicuous element, increasingly so as one goes southward into the Peninsula. Huge vines of wild grape are frequently suspended from the hammock trees and a well-developed shrub stratum usually occurs. Among the commoner of the shrubs and lianas are: *Smilax lanceolata*, *Gelsemium sempervirens*, *Rhus copalina*, *Rhus radicans*, *Callicarpa americana* and *Vitus rotundifolia*. The partridge berry *(Mitchella repens)* frequently covers considerable patches of the hammock floor and a heavy leaf mould is often developed. In the red-clay residual soils of northwest Florida, a more northern type of mesophytic woods is developed. Here the beech *(Fagus grandifolia)* forms a moderate to considerable proportion of the hammocks, and deciduous oaks and red bud *(Cercis canadensis)* are more common.

The magnolia, laurel oak, holly and other trees of the mesophytic hammocks are evergreen. Their leaves and the omnipresent Spanish moss form a considerable shade, even in the winter months, and in summer the shade is dense and nearly continuous. There is an abundance of rotten wood that exhibits a moist, but not sodden, type of decay.

14. *High Hammock.*

The high hammocks are associated with a low water table, due either to deep sandy soil or upland conditions. They intergrade with the magnolia

hammocks on the one hand and with high pine and oak scrub on the other. One of the characteristic trees is the live oak *(Quercus virginiana)*, although this is not confined to the high hammocks. Among others are the red oak *(Q. falcata)*, post oak *(Q. stellata)*, *Hicoria alba*, sparkleberry *(Batodendron arboreum)* and dogwood *(Cornus florida)*. The trees are rather widely spaced and the ground has a considerable daily exposure to sunlight. There is a larger growth of annuals than is exhibited by the more shaded hammocks and a considerable development of shrubs. The soils become quite dry in the dry season and there is a comparatively small retention of leaf mould and humus. Fire and pasturage are serious checks on the development of the high hammocks and nearly all of them suffer, at least occasionally, from one or both. As compared to the magnolia hammocks, they have a much less dense and uniform shade, a lower and more variable humidity, drier soil, a greater fluctuation of soil temperature, and dead wood usually soon enters into a state of dry decay.

B. Pine Lands

Areas dominated by pine forests are the most extensive of all northern Florida vegetational formations. A great variety of pines occurs in Florida but the long-leaf pines, *Pinus palustris* and *Pinus caribaea* are the dominant trees of the typical pine formations. The short leaf pines, *Pinus taeda* and *Pinus echinata*, although abundant in most sections of northern Florida, particularly in the western portion, and forming a considerable element in the various types of hammocks, only locally form the dominant trees of any save second-growth formations.

The long leaf pine formations are usually subdivided into pine flatwoods and "high pine," but there are considerable areas of intergrading and both the flatwoods and high pine have been long and extensively exploited and modified by lumbering, turpentining, pasturage and fire.

15. *Pine Flatwoods.*

These form low, level, monotonous areas along both coasts and over much of the inland regions and are associated with sandy soils under-layed, at a slight depth, either by a definite hardpan or by sub-soils that are slowly pervious to water. Consequently, the flatwoods become very wet or even inundated for long periods during the rainy season and are frequently parched and dry during the dry season. The larger trees are a practically pure stand of long leaf pines, save that frequent shallow depressions are the sites of cypress ponds and "bays." Two general types of flatwoods can be distinguished, although here again transitional and intermediate phases occur. The various types are associated with soil differences, particularly those of the subsoil which ranges from impervious hard-pan to less impervious clays.

The flatwoods, developed upon hard-pan soils, (Leon and perhaps other

soil series) show the most xerophytic type of vegetation. The pines are small and slender and the undergrowth is dominated by dense thickets of saw-palmetto *(Serenoa serrulata)* with a considerable development of gallberry *(Ilex glabra)* and huckleberry (*Vaccinium* sps. and *Gaylussacia* sps.) in the lower areas and the vicinity of cypress ponds and bays.

Flatwoods with clay subsoils show less extreme fluctuations of moisture and this is reflected in the considerable differences shown by the vegetation. The pines are taller and more robust, saw-palmetto is small and scant or absent and gallberry is rarely well developed. Wire grass and sedges are abundant, often forming an almost complete grassy covering between the trees, and giving this type of flatwoods a park-like appearance.

In both types, the surface soil and soil water is definitely acid, more markedly so in the hard-pan type, and the zones of more lush vegetation that border most of the cypress ponds and bays have a good development of sphagnum, pitcher plants (*Sarracenia* sps.), sundew *(Drosera capillaris)* and ground pine (*Lycopodium* sp.) as well as grasses, sedges, ferns and low huckleberry bushes.

16. *High Pine.*

High pine formations are associated with well drained, sandy soils and usually show the best developed examples of *Pinus palustris*. The forest is open with the larger trees rather widely spaced and its floor is exposed to sunlight for much of the day. Turkey oak *(Quercus catesbei)* often forms a scattering understory and there is a considerable development of wire grass and other herbage, that is most conspicuous in the rainy season. Two very characteristic features of the high pine formations are the frequent burrows of the gopher turtle *(Gopherus polyphemus)*, and the sandy mounds thrown up by the Florida "salamander" (*Geomys tuza*, a pocket gopher), both good indicators of a comparatively deep water table and sandy soils. The slight shade, dry soil and free air movement combine to produce a high evaporation rate. Humus tends to accumulate very slowly, even when not destroyed by the ground fires to which most high pine areas are periodically subjected, and fallen wood undergoes a slow, dry decomposition.

17. *Turkey Oak on Cut-Over High Pine Lands.*

So much of the high pine has been completely or largely cut-over, with natural reforestation prevented by ground fires and other causes, that extensive areas of formerly high pine forests are occupied by a now dominant growth of turkey oak. The turkey oak is deciduous and during the winter and the spring dry season these second-growth areas are exposed to full sunlight and free air movement and become drier than high pine formations of similar soils and topography. The herbage becomes scantier than in the pine forest; "salamander" mounds are perhaps more numerous, at any rate more

conspicuous, but the burrows of the gopher turtle often decrease or disappear. Except for the sand scrub these turkey oak second-growths are subject to the highest dry season evaporation rates and soil temperatures of any extensive habitat in northern Florida.

18. *Sand Scrub.*

Still more xerophytic than the turkey-oak second-growth of the cut-over pine lands are the areas known as scrub. Scrub is most extensively developed in the lake and lime sink regions but examples occur in most of the counties of northern Florida and not infrequently small areas of scrub occur as abrupt islands between swamps or between a swamp and a hammock. Here the vegetation consists of stunted bushes and scrubby trees, of which the evergreen oaks, *Quercus geminata* and *Q. myrtifolia* and the rosemary, *Ceratiola ericoides*, and a scattering growth of spruce pines, *Pinus clausa*, are common and typical. Most of the vegetation tends to grow in dense low patches between which are areas of bare and nearly white sand. The water table is deep below the surface, which shows a great diurnal range in temperature. Here the evaporation rate and the mid-day soil temperature are the highest for any natural habitat of northern Florida.

Of the 18 types of inland habitats discussed, three have no species of crane-fly typically associated with them. Of these three, the lower streams not infrequently provide the conditions required by certain swamp, marsh, or lake margin species, but the driest of the terrestrial habitats, the "turkey oak second growth" and the "sand scrub" are not inhabited by any stage of any species.

Some Restricted Areas of Particular Interest

The various habitats often have sharp boundaries or abrupt transitions to very different sorts of situations. Frequently, the region of such a transition, or a restricted area which combines many of the features of several habitats, has a peculiarly rich crane-fly fauna.

THE DEVIL'S MILL HOPPER, ALACHUA COUNTY

This is a large, deep limestone sink about seven miles northwest of Gainesville. Formerly, it was surrounded by a virgin stand of long-leaf pine but this was cut some seven years ago and is now rapidly being replaced by turkey oak, but extensive areas of hammock, swamp and flatwoods occur within half a mile. The sink is roughly funnel-shaped, about 150 yards in diameter at the brim, 110 feet deep, with a nearly circular, flat bottom, perhaps 20 yards in diameter. A small brook flows into the sink from the west and within the sink itself a dozen small rills arise from springs on the higher slopes and tumble down the steep sides in miniature cascades and rapids. All of this water ordinarily flows out at the bottom by way of an underground

stream, so that only a small, shallow pool occupies one side of the bottom. But, from time to time, either an increase of inflow, an obstruction to the outflow, or a combination of the two, result in flooding the bottom of the Mill Hopper so that water may stand at a depth of 15-20 feet for several months at a time.

The sides of this sink-hole bear a luxuriant mesophytic hammock vegetation and the deep shade and the shelter from wind produce a comparatively high humidity. The south and west slopes are densely grown with tall ferns and about many of the springs and rills, areas of saturated earth support a rich growth of Jack-in-the-Pulpits, while the firmer clay and limestone exposures are covered with dense mats of liverworts and mosses. Several of the springs and many of the diffuse seepage areas derive their water from disintegrating strata of soft limestone and are markedly basic (pH 8.3-8.7), as are many spots of boggy, lime-filled earth; while close-by, other diffuse rills, seeping through accumulations of silt and humus, have a circum-neutral or even definitely acid reaction (pH 7.6-6.25).

Here, within an area of a few square yards, may occur many distinct types of habitats for immature crane-flies: damp soil, earth saturated with either stagnant or flowing soil water and ranging from slightly acid to basic, flowing water, thin cascades and trickles over sludge- and algae-covered rocks, wet rocks and cliffs, and wood in all stages of wet decay, often bearing rich growths of fungi or mosses and liverworts. For the adults, there is shelter from light and desiccation. Eighty species of crane-flies have been taken from this area of less than three acres and one of these, *Polymera rogersiana,* is, so far, known from no other situation, although fairly numerous here.

THE "TORREYA" RAVINES OF LIBERTY COUNTY

Along the eastern side of the Apalachicola River, in western Florida, is a series of high bluffs into which a number of small streams have cut narrow, steep-sided valleys, often well over 100 feet deep. Botanically, the cool humid ravines of this very restricted area have long been of great interest as the habitat of two endemic and very disjunct coniferous trees, *Tumion taxifolium* ("Torreya," savarn or stinking cedar) and *Taxus floridana* (Florida yew). Many other trees of these densely wooded ravines are of interest in that they occur in but a few or no other places in Florida and are only to be found commonly, elsewhere, much farther north. In fact, the general aspect of the flora of these ravines reminds one of regions in the Piedmont, despite the inclusion of a number of typical Florida plants. Beeches *(Fagus grandifolia)* vie with magnolia, spruce pines *(Pinus glabra)* and Torreya as the most dominant of the trees and these, with sweet gum, yellow poplar *(Liriodendron tulipifera),* white oak, sugar maple *(Acer floridanum),* hornbeam, red bud, holly and needle palms *(Rhaphidophyllum hystrix)* make up the bulk of the

more conspicuous vegetation. A heavy leaf mould is present and herbs are scarce but *Mitchella repens, Trillium* sp., *Sanguinaria canadensis, Hepatica triloba,* and *Uvularia* sp., occur here and there on the steep slopes and contribute to the northern aspect of the vegetation.

Small sandy bottom brooks flow along these ravines and often pass into short swampy reaches where they wander through tangles of standing and fallen vegetation and over deposits of rich organic silt. Near the bottom, springs and seepage areas are common and wet rotten wood, fungi, mosses and liverworts are abundant.

The fauna of these ravines is as surprising and interesting as their flora, for here a number of animals reach their southernmost limits, frequently disjunct from the remainder of their ranges. In the Amphibia, Crustacea, Odonata, Ephemerida and Orthoptera a number of unexpected, northern species or species with distinct northern affinities have been discovered and among the crane-flies more than a dozen species are found that have been taken nowhere else south of the Piedmont region.

RED CLAY HILLS OF NORTHWESTERN FLORIDA

In Jackson, Gadsden, Leon and Jefferson counties there occur somewhat varied types of rolling hills and bottoms with steep wooded hillsides and a rich development of hardwoods and pine that resemble certain parts of the Piedmont region of Georgia and the Carolinas. Beeches and large deciduous oaks form a considerable part of the forest; the upland woods are more mesophytic than the high hammocks of the peninsular region; and the lowlands have either rich hardwood swamps or wet boggy woods. Except for a considerable element of short leaf pines, the hammocks have a high proportion of deciduous trees. Here, again, several northern or upper austral crane-flies find the southern limits of their ranges.

ASH AND GUM SWAMPS OF JACKSON COUNTY

Locally, in numerous parts of the narrow area drained by the Apalachicola River and its tributaries, there are deep swamps of tupelo gums *(Nyssa ogeche* and *N. uniflora)*, titi (Cyrilla and Cliftonia), and ash (*Fraxinus* sps.). Although a number of these swamps or bays have been collected from, only one (a narrow but extensive swamp along Blue Spring Creek in Jackson County) has been worked in any detail. Here a dense swamp of ash, tupelo gum, sweet gum and red maple, with some denser patches of titi, borders the east side of the clear calcareous creek and extend to the beech-grown slopes of the valley sides. A fringe of herbage occurs along either margin but most of the interior has a bare, boggy floor strewn and imbedded with wood in all stages of wet decay; and the numerous rills that rise from springs along the foot of the valley slopes, meander through or

become lost in the deep black muck and stagnant lagoons. Two species have their Florida records confined to this or similar swamps and a number of species, rare elsewhere in Florida, have been taken here in numbers during successive years.

THE CRANE-FLY FAUNA OF NORTHERN FLORIDA

Previous Work on the Crane-Flies of Florida

Aside from a few scattered records by earlier workers and a brief collecting trip in northeastern Florida by Osten Sacken, in the spring of 1858, most of the knowledge of the crane-fly fauna of the state has been due to two published lists of the "Diptera of Florida" by Johnson (1895, 1913). These included the older records of Say, Wiedemann, and Osten Sacken but were largely based upon Johnson's own collecting—in the years 1880-1888, 1891, and 1894, upon the collections made by Annie Trumbull Slosson during her winter visits to Florida for a period of many years, upon material in the U. S. National Museum and the American Museum of Natural History and upon records furnished by M. C. Van Duzee, based upon a collection he made in the spring of 1908.

Other papers that have contained references to or descriptions of Florida crane-flies are those of Alexander (1914, 1916, 1920a, 1925, 1926, 1926a, 1926b, 1927, 1927a, 1927b, 1929, 1929a, 1931), Dietz (1918), and Rogers (1926, 1926a, 1927, 1927a, 1927b, 1928, 1932).

The Florida List

Johnson's second paper on the Diptera of Florida (1913) lists 36 species of Tipuloidea. To these, Alexander's three earlier papers (1914-1920) added nine species, and Dietz (1918) described *Pachyrhina costomarginalis*, which in the present paper is relegated to synonomy as the male of *Nephrotoma suturalis*, previously recorded by Johnson. My own collecting, 1922-1932, has resulted in a list of 127 species that includes all but eight of the 45 species previously recorded. Of these eight species, four are accepted as undoubted or very probably correct records.[3] This makes a state list of 131[4] species, of which 128 occur in or have been recorded from northern Florida as limited in the present paper.

Derivation of Florida Fauna

The crane-fly fauna of Florida consists of northern, neotropical and endemic elements. Of these, the northern species are in the majority, and

[3] Four species recorded by Johnson (1913) are regarded as very doubtful: *Limonia morioides* and *Limonia pubipennis*—recorded as *Furcomyia*—are not at all regional and the characteristic habitats of these species are not found in Florida; *Limonia adusta* is not at all regional and this record probably pertains to *Limonia osceola; Nephrotoma ferruginea* is not regional and this record probably pertains to the dimorphic male of *Nephrotoma suturalis.*

[4] The Florida fauna is seen to be relatively poor when contrasted with those of the northern and Appalachian Highland states that have been more or less intensively studied: New York (Alexander 1919, 1922, 1924, 1929b-c), 318 species; New England (Johnson 1925 and Alexander 1925a, 1927c, 1930), 318 species; District of Columbia (Alexander and McAtee 1920), 201 species; Michigan (partial preliminary list), more than 200 species; Cumberland Plateau (one summer, Rogers 1930), 154 species; mountains and Piedmont of North Carolina (partial preliminary list), more than 200 species.

markedly so in northern Florida. Twenty-six species are endemic or extend slightly beyond the political boundaries of Florida into the extreme southern coastal plain and here, again, the endemic species of apparently northern relationships predominate over those derived from neotropical stocks.

The geographic distribution of each species is summarized in Table V but the following tabulation will show the relative importance of the several elements that comprise the Florida fauna:

I. Northern species belonging to northern genera, subgenera or groups, that reach their southern limit in Florida.
76 species—about 58% of total fauna.

II. Northern species belonging to predominantly neotropical groups, but the species in question reaching their southern limits in Florida.
15 species—about 11% of total fauna.

III. Endemic or extreme southern coastal plain species whose relationships are with northern groups.
19 species—about 14% of total fauna.

IV. Endemic and southern coastal plain species whose relationships are with neotropical groups—one of these, *Orimarga wetmori*, is confined to southern Florida.
7 species—about 5% of total fauna.

V. Neotropical species, reaching their northern limits in Florida or in southern states north of Florida—two of these, *Limonia reticulata* and *Teucholabis myersi*, reach their northern limits in southern Florida.
12 species—about 9% of total fauna.

VI. Cosmopolitan species.
2 species—about 1.4% of total fauna.

Florida's connection with the mainland of North America since at least late Miocene times and the continuous existence of a marine barrier from Neotropica, save by way of Mexico and the northern Gulf Coast, no doubt account for the relative proportion of northern and neotropical elements of the crane-fly fauna. Less obvious is the reason for the total absence of many northern species. One of the most important barriers to the northern groups, the ranges of which extend into the Piedmont Province of Georgia and the Carolinas, is the monotonous, low-pine lands of the southern coastal plain with their dearth of clear, fairly rapid, pebble-bottom streams and of cool seepage areas with rich organic soil, and the scarcity of hardwood formations with persistent cool, moist shade, humus and leaf mould. All three of these provide larval habitats for large groups of northern species and genera. Except for gravel-bottom streams, restricted local areas of such habitats reoccur in northern and northwestern Florida and show an almost wholly northern crane-fly fauna, many of the species apparently disjunct from the remainder of their ranges by the width of the south Georgia coastal plain.

Most of the northern species that occur in Florida are associated with hardwood formations, hammocks, swamps, and wooded ravines and sinkholes, or with typically wooded seepage areas and spring-fed streams. As

one goes southward into the state the number of northern species rapidly declines with the decrease in hardwood hammocks and seepage areas.

Temperature probably has a lesser direct effect as a barrier than topography, vegetation or the prolonged winter dry season, but may account for the absence of *Trichoceridae*, a holartic family, in which, in the northern states (extending as far south as the southern edge of the Piedmont region in Georgia), the adults are usually confined to the season between the first and last frosts of the winter, and, possibly, the *Cylindrotominae* and the genera Prionocera, Ctenophora and Tanyptera, all Holartic groups with larval habitats that apparently could be provided by the hammocks and swamps of northern Florida.

Speciation in Florida Crane-flies

Several northern species are replaced in Florida, and often in the extreme southern coastal plain, by Floridian subspecies. The best known instance is *Limnophila macrocera suffusa* which replaces *Limnophila macrocera*, south of the Piedmont Province, in Georgia, South Carolina, and Florida. Other probable instances, that require larger series from the southern Piedmont and southern coastal plain before they can be definitely established, are: *Pilaria arguta* may prove to be a southern swamp- and "bay"-inhabiting race of *Pilaria recondita*, the ranges of the two overlapping in northern Florida; and *Nephrotoma suturalis* is probably a southeastern subspecies of *Nephrotoma ferruginea*, replacing the latter south of the Piedmont and extending throughout Florida.

Several other northern species that apparently extend into Florida require the comparison of Florida specimens with large series from the remainder of their ranges. Among the species in which Florida representatives appear to show slight but constant differences from northern (Michigan, Indiana, and Appalachian Highland) specimens are: *Oropeza obscura*, *O. sayi*, *Tipula duplex*, *Tipula triplex*, *Tricyphona inconstans*, and *Erioptera (Ilisia) venusta*.

Several species, now classed as endemic, may occur in other regions. This has already been found true for *Ulomorpha rogersella* Alexander, described from western Florida but found in the spring of 1930 to be far more abundant in the mountains (4,000 feet) of southwestern North Carolina. However, most of the species now regarded as endemic appear to be correlated with characteristic or peculiar Florida or southeastern habitats. The most typical crane-flies of the extensive flatwoods formations are *Tipula ludoviciana* and *Tipula osceola*. The only characteristic crane-fly of the high pine forests is *Tipula oxytona* which also occurs commonly in the typically Floridian, high-sandy hammocks. Another endemic, *Limnophila osceola* is characteristic of flatwoods cypress ponds and "bays" while *Erioptera seminole* has only been taken from the highly acid "bays" and bog streams. Of the endemics of southern relationships whose habitats are well known, *Limonia*

vanduzeei is a typical inhabitant of grassy-flatwoods cypress-pond margins. *Limonia subapicata* may be restricted to the wet or moist hammocks where *Pinus glabra* occurs, and *Polymera rogersiana* is at present known only from areas of markedly basic seepage in sink-holes.

FACTORS AFFECTING ECOLOGICAL DISTRIBUTION

THE LIFE CYCLE

A knowledge of the habitat distribution of the crane-flies is made particularly difficult by their holometabolous life cycle. The adults and larvae have few habitat requirements in common and these active stages are connected by egg and pupal stages which often introduce additional requirements.

The length of the life cycle varies from several months to a year. In most of the *Tipulinae* there is single generation per year; in many of the *Limoniinae*, under favorable conditions of temperature and moisture, there may be two, and even three generations per year. With a few exceptions, and these mainly among the endemic and coastal plain species, the occurrence of the successive stages does not have a clear cut seasonal relationship but varies widely with fluctuations in climate and with minor differences between similar types of habitat; even for most of the species that require the major portion of a year for the life cycle, there is a marked overlapping of generations. The absence of definite seasonal distribution is no doubt explained by the absence of clearcut seasons, and yet, certain of the endemic species, notably *Tipula osceola, T. oxytona, Molophilus floridensis* and *Limnophila osceola*, have a definite seasonal distribution.

The Adult

Although definite knowledge of the duration of the life of adults in nature is difficult to obtain, observations on specimens in breeding cages, as well as repeated field notes on emergence and disappearance within isolated habitats, indicate that few of the smaller *Limoniinae* live longer than two weeks and few of the *Tipulinae* attain an age of three weeks. For many species, and the huge majority of individuals of all species, adult existence is far shorter than these estimated maxima. Barring interruptions due to low temperatures or occasional periods of widely prevalent low humidity, the essential adult functions of mating and oviposition are completed within two-four days of emergence.

For most of the species, the greater part of adult life is spent quietly resting within some sheltered portion of the general habitat. The resting places vary, not only with the species and type of habitat, but with meteorological conditions and the time of day. Many species, including a number of inhabitants of open hammocks, rest on the top surfaces of leaves of the herbage and lower shrub strata; other species, including most of the inhabitants of dank shaded situations, cling to the underside of the leaves or on the lower

stems of rank herbage: inhabitants of marshes and open grassy situations usually rest deep within the grass and sedge stratum; and a number of species, including several in the genus Tipula, some of the larger species of Limonia, and *Gnophomyia luctuosa* rest on shaded tree trunks, usually in close contact with the surface. Still other species, notably *Bittacomorpha clavipes,* most Oropeza, *Diotrepha mirabilis* and several species of Tipula, hang limply from some overhead support, often a strand of spider web, within such dim, humid recesses as are provided by hollow trees and logs, overhanging banks, and rank fern hummocks. When the habitat is unusually damp or where local conditions provide such markedly cool, moist spots as wet shaded cliffs and mossy banks, many species rest in relatively exposed positions but, when high evaporation rates prevail these same species retreat into more protected situations, responding positively to all factors that decrease evaporation: higher humidity, shelter from air movement, and reduced insolation.

Comparatively little is known about the feeding habits of the adults. Nearly all species that have been reared, were able to mate and oviposit without food and, although feeding practically doubles the life of the adults and tends to prolong somewhat the period of oviposition, lack of food does not appear to decrease the number of fertile eggs oviposited. *Limonia canadensis* and *L. rostrata* are more frequently observed feeding in nature than any other species and yet, unfed pairs of *L. rostrata* have frequently mated in the breeding cages and, in most instances, the female laid her full complement of eggs a day or more before she died. On the other hand, representatives of some thirty-three species in the breeding cages fed for several minutes at a time when given dilute sugar solution. More than a score of species have been observed feeding in the field. In nature, the usual food appears to be the nectar of flowers, but *Gnophomyia luctuosa* has been seen several times feeding on sweetish exudate from the rotting heartwood of living trees, *Brachypremna dispellans* and *Limonia domestica* feed on the juices of broken, overripe fruit as well as on nectar, and several species of Tipula have been observed with their mouth parts applied to swollen, mucilaginous leaf buds of an unidentified, deciduous tree. These buds when moistened with saliva had a perceptibly sweet taste.

The most frequently observed activity of the adult is the mating behavior. This varies markedly in detail among the various species. The actual finding and mating with the female appears to depend almost wholly upon contact. Olfactory or similar stimuli may activate the males and initiate a series of random movements that increase the chance of contact but a sexually active male may come within a few millimeters of a female and make no effort to copulate unless some part of his body chances to touch hers.

In most of the *Tipulinae* and many species of the *Limoniinae,* the males,

which have a pupal period of one or two days shorter than the females, spend most of their active hours searching for emerging and callow females. Frequently one or more males may be observed in slow sprawling flight, touching the surface of the ground at frequent intervals, over spots where adults are still emerging. Considerable areas are explored and when the male comes into the vicinity of a pupal, emerging, or teneral female, his movements become much more rapid and his contacts with the surface more frequent and more closely spaced. Once contact is established, the female is seized and mated with, or if she has not yet emerged, the male stands over the projecting pupa case, ready to seize her abdomen in his forceps as soon as it is exposed. Often two, three, or four males may be found above the emerging female, all striving to obtain the copulatory clasp. In many species it is relatively rare for a female to become fully mature before mating.

Another type of mating behavior brings about contact between the sexes while both are in flight. Several or all of the species of Eriocera, Tricyphona, Elephantomyia, Ormosia, Erioptera and other genera, form mating swarms, the form, time and duration of which vary with the species. Usually at twilight, and always under humid, diffusely lighted conditions, a few or many hundreds of flying males zigzag back and forth in a limited but shifting space; individual females flying into the swarm, come into contact with the males and, pairing, fly *in copulo* to a near-by resting place where mating is completed. *Tipula caloptera, Trycyphona inconstans, Limonia distans*, and a few other species, show both types of mating behavior.

The oviposition of fertile eggs may begin within two hours of copulation and females that have mated at dusk, usually begin oviposition the same night. Females in large, out-of-door breeding cages usually laid their eggs, in approximately equal fractions, on two or three successive nights but in several instances a series of cold nights, 10°C. or somewhat lower, interrupted oviposition for 2-5 nights in succession. These interruptions occurred between copulation and the first oviposition as well as between the beginning and completion of oviposition.

Eggs are deposited in the habitat that is to be occupied by the larvae, or, at least, by the first instar. Whenever observed in the field, the actual oviposition was preceded by the female probing about with her ovipositor to find a suitable spot. Apparently, a very definite choice is shown for many more places are probed than have eggs deposited in them.[5] In each instance, the eggs were deposited well beneath the surfact of the chosen medium and could only be found by a painstaking examination of the material to a depth of 2-3 mm.

Excepting *Bittacomorpha clavipes*, all species that have been observed, appear to lay one egg at a time, although successive ovipositions may be in

[5] The actual laying of the eggs is made evident by the dilation of the bases of the ovipositor and a sliding motion of the upper valves against the lower valves.

such proximity that a dozen eggs are placed within a radius of 15 mm. or less. The number of eggs varies both with the species and with individuals of the same species,[6] averaging about 150-200 for many of the *Limoniinae* and 250-350 for the *Tipulinae* and the *Ptychopteridae*. In nearly all instances where the eggs were laid within the breeding cages, whether by females that had been reared or by females captured in the field, 10-20% of the eggs failed to hatch. As far as known these eggs were exposed to precisely the same conditions as those that produced living larvae, and are believed to have been infertile.

The Eggs

As far as known, all crane-fly eggs begin to develop as soon as laid, but the time required for development varies somewhat with the species and is markedly modified by temperature. The following durations of the egg stage, from oviposition to hatching, is based on eggs placed on wet filter paper in petri dishes and kept at out-of-door temperatures. There was usually a variation of 10-15% within each clutch of eggs: *Bittacomorpha clavipes* (March and May), 4-5 days; numerous Limoniinae of the genera, Diotrepha, Limonia, Pseudolimnophila, Polymera, Antocha, Erioptera and Elephantomyia (January, February, April), 6-10 days; *Tipula tricolor* and *Oropeza obscura* (March, April), 13-16 days; *Tipula caloptera* (December—very warm, May) and *Nephrotoma suturalis* (May), 6-8 days. In other instances, intervals of lowered temperature greatly prolonged the duration of the egg stage for some of these same species.

The Larva

At hatching, the larvae are nearly transparent with a thin delicate integument, only the mandibles appreciably chitinized, and the specific markings of the later instars faintly, if at all discernible. The newly hatched larvae of *Tipula caloptera*, one of the largest species in North America, are about 2.5 mm. long and 0.35-0.4 mm. in diameter. The fully grown larvae average about 45 mm. long and 4-6 mm. in diameter. The newly hatched larvae of the smaller species are somewhat under 1 mm. in length and about 0.1-0.13 mm. in diameter.

Under favorable conditions of temperature, moisture and food, growth is rapid and apparently continuous, but periods of low temperature, deficient moisture, or deficient food greatly prolong the time required for development. The following minimal periods for larval development are based upon breeding cage records, out of doors, or in an open, unheated building, with as nearly as possible optimum conditions of food and moisture: *Diotrepha mirabilis*, 13-15 weeks; *Limonia cinctipes*, 20-24 weeks; *L. rostrata*, 8-10 weeks; *Epiphragma solatrix*, 20 weeks; *Pseudolimnophila contempta*, 12-15 weeks; *Polymera rogersiana*, 10-12 weeks; and *Teucholabis complexa*, 15-16 weeks.

[6] Breeding cage observations on *Diotrepha mirabilis*, *Limonia cinctipes*, *L. rara* and *L. subapicata* show that the number of developed eggs is greatly modified by the food supply of the older larvae.

Field observations and incomplete but overlapping breeding cage records indicate that the larvae of *Tipula caloptera* require 7-10 months for development and the larvae of *T. abdominalis* somewhat longer, probably 9-10 months under favorable conditions.

The number of larval instars is not positively known for any species that occurs in Florida. Cameron (1928) in rearing *Cylindrotoma splendens,* one of the few crane-flies in which the larvae live in a visible situation on the leaves of a herbaceous plant, found an apparently constant number of 3 instars—the usual number throughout the Diptera. My own incomplete observations on several Florida species indicate that there may be 4 or 5 instars and that the number is not necessarily constant.

The food and feeding habits of the various species are extremely diverse. The majority feed upon plant material and of these, a large group feeds on living tissues ranging from algae and fungi to the roots and stolons of herbaceous plants; another large group ingests decayed plant tissues but it is probable that their actual food consists of fungi and other microscopic flora. Many of the dwellers in mud and saturated silt ingest considerable amounts of the habitat medium and are probably to be classified as scavengers. Other silt inhabitants feed largely on living plant tissues. A considerable number of the silt inhabiting larvae are carnivorous, as are several of the definitely aquatic species. The food of the larvae of each species, as far as known, is given in the annotated list, pp. 44-61.

The larvae of a number of species, including nearly all members of the large genus, Limonia, construct tubes within which they live, the tube usually leading from some protected crevice to a feeding place. These tubes are formed from a secretion of the salivary glands and are usually thin and delicate but in some species become opaque and have a coating of fine, wood debris. The tubes are added to as the larva moves to new sources of food supply and the older disused portions quickly disintegrate so that the length remains fairly constant, some 3-6 times the length of the larva's body. Some of the inhabitors of dense mosses, rotten wood, and compact or moderately dry, plastic soils, form more or less permanent burrows, that lead to protected feeding places or from which they emerge to feed at night.

The Pupa

The change from larval condition to the pupal stage is somewhat gradual. Aquatic larvae migrate to a protected situation above the water line some time before pupation. Most of the tube-forming species construct a second inner capsule near the mouth of the larval tube. Larvae that live in soil and rotten wood make a short tube or burrow opening to the surface of the soil or log. Most of the mud- and silt-inhabiting species make no visible preparation other than approaching close to the surface, but *Tricyphona inconstans* constructs a short vertical burrow, lined with material like that formed by

tube-building species, and projecting above the surface of the saturated soil (seepage area or rill margin) like a miniature crayfish chimney. The larva becomes almost totally quiescent some hours before any outward signs of pupation are discernible and then faint outlines of the cephalic half of the pupa become visible before the larval skin is shed. The latter splits or breaks in the thoracic region and is gradually pulled and worked caudad by the spasmodic movements of the pupa. In species that form tube-like cases, cocoons (Atarba), burrows or earthern chambers (Dicranophycha) for the pupal stage, the molted larval skin and head capsule may be found as a crumpled pellet just below the cauda of the pupa.

As in many nematocerous Diptera, the crane-fly pupa is capable of considerable movement and pupae not enclosed in a case or cocoon move up and down in their burrows in response to various stimuli, such as, light, temperature, and contact. Near the end of the pupal period spasmodic and rythmic movements serve, thanks to the downward projecting spines of abdominal annuli, to force the pupa to the surface of the earth, wood or moss where its cephalic third or half projects into the air.

Like the egg and larval stages, the duration of the pupal stage varies with the different species and is affected by temperature and probably other physical factors, but for all Florida species in which the length of the pupal stages is known, and, within the limits of normal Florida weather, duration of the pupal stage lies between 3.5 and 10 days.

Emergence of Adult

Emergence of the adult is preceded by the rythmic movements just described that cause the pupa's cephalic end to project from the surface, but the caudal portion remains implanted in the soil, or encased in the cocoon or old larval tube. Once in this position, the dorsum of the thorax soon splits longitudinally and the head and thorax of the imago are quickly freed. A back-and-forth, rocking motion of the free part of the adult body soon begins and gradually lifts the abdomen from its case and draws the legs and wings from their sheaths. As soon as the legs are freed, the fly bends forward to obtain a foothold and the abdomen is then wholly withdrawn from its case. In some species, the freeing of the abdomen and legs appears more difficult and is largely effected by rythmic pulsations of the abdomen which, erect, turgid, greatly elongated, and projecting as a vertical cylinder, is slowly forced out of its enclosing pupal skin and so draws the legs from their cases by the vertical pull on their bases.

When free, the soft, swollen adult rests near the empty pupa skin until its abdomen approaches normal size. Complete disappearance of the teneral condition may take several hours but normally flight is possible within an hour, in some species within a very few minutes. This period of emergence appears to be the most precarious time of the entire life cycle. Numerous

enemies, notably spiders, ants and predacious beetles prey upon the exposed pupae and callow adults. Adverse weather conditions, such as sudden hard rains, occasionally result in heavy mortality.

Enemies

Alexander (1919: 776-777, 1920a: 721-734) has given an extensive summary and discussion of all the data he could gather on enemies of crane-flies, including records obtained by examination of a huge series of bird stomachs by the U. S. Biological Survey. In Florida representatives of all predacious and parasitic groups listed by Alexander, doubtless prey upon crane-flies but positive records are largely confined to scattered observations in the field. Many larvae show gregarine infestation of the digestive tract, particularly of the hind gut, but there is no evidence that this is pathogenic. Death from fungus attack (Phycomycetes?) has been occasionally noted in a number of species whose larvae inhabit semi-aquatic situations *(Tipula caloptera, Limonia (G.) rostrata, L. (G.) canadensis* and *Pseudolimnophila contempta)* and in several species in which the larvae inhabit wet, rotten wood and the higher fleshy fungi *(Limonia cinctipes, L. rara, L. macateei* and *Elephantomyia westwoodi)*. Usually, it is the pupa but occasionally an adult, presumably teneral, that is the victim of fungus attack and is found covered with filaments or fruiting bodies of the fungus.

Parasitization by insects is remarkably rare. In fourteen years of collecting and rearing adult and immature stages, I have only twice observed insect parasites. A large dipterous larva was taken from the abdomen of an adult, female *Nephrotoma ferruginea* in Michigan, and, in Florida, fifteen braconids, nearly fully colored and ready to emerge, were taken from a female pupa of *Oropeza sayi*. The integument of the pupa was intact but empty of all host tissue and the space was completely filled by the parasites. Other pupae and larvae of *O. sayi*, taken from the same moss mat on the same day, showed no signs of parasitization.

Spiders are frequently observed preying upon the adults. Various dark, cursorial spiders that abound in moist situations, on wet rocks, in mosses and liverworts, about the margins of ponds and brooks in the leaf mould and sphagnum of hammocks and swamps, are often seen feeding upon crane-flies, teneral individuals and ovipositing females forming a considerable part of their victims. Web-building spiders, especially those which spin webs among the tall grasses and sedges of marshes and low grassy flatwoods, also take a considerable number of adults.

Of the predacious insect enemies, robber-flies and dragonflies appear to be most important. I have observed a common, large reddish species of Deromyia capture *Brachypremna dispellans, Tipula mingwe*, and *Epiphragma solatrix* on the wing, taken *Ommatius tibialis* Say feeding upon *Diotrepha mirabilis* in some numbers and frequently noted small slender robber-flies of

the subfamily *Leptogasterinae* capturing various species of Erioptera, Gonomyia, and Teucholabis, just above the herb stratum of damp, shaded hammocks.

As far as frequency of observation goes, however, tree frogs, particularly *Hyla cinerea* and *Hyla gratiosa,* account for the destruction of more adult crane-flies than any other enemy. On nights when the adults are feeding in large numbers on mango, orange, oleander, and privet blossoms, many of the flower clusters have one or more attendant tree frogs alertly snapping up all insects that come within reach. A *Hyla cinerea* was once observed to take four crane-flies *(Geranomyia* sp. and *Rhipidia domestica)* in less than five minutes. *Acris gryllus* has been seen feeding upon *Pseudolimnophila luteipennis* and *Limonia distans* and the haunts of various species of Hyla, Acris and Pseudacris, are the same shaded retreats frequented by many crane-flies. Stomach examinations of several hundred specimens of *Rana catesbiana, R. grylio* and *R. clamitans,* taken in Alachua County, showed that the first two species occasionally fed on adult crane-flies and the third fed upon them in considerable numbers.

The larvae are preyed upon by Tabanid larvae and the larger, predacious crane-fly larvae. Larvae of Tabanus and Chrysops have been known to feed upon the larvae of various species of Tipula, Pseudolimnophila and Limnophila and of *Polymera georgiae,* while the larvae of Eriocera and Penthoptera capture other crane-fly larvae and are probably cannibalistic.

Among the vertebrates, birds probably form the chief enemies of the immature stages. Various species of birds are frequently observed feeding in spots where larvae and pupae are abundant but I have never made any stomach examinations. Signs of moles and shrews are often evident in the larval habitats of soil inhabiting species but the only mammals for which I have conclusive evidence of feeding on crane-flies are raccoons, which in northern Florida apparently devour considerable numbers of the larvae of *Tipula abdominalis* and *T. caloptera,* and the skunk *(Mephitis nigra?),* which in southern Indiana, has been observed feeding on the larvae and pupae of *Tipula cunctans.*

Habitat Requirements of the Adult

Prolonged and repeated observation in field and laboratory and numerous simple experiments indicate that the main factors limiting the habitat of the adult are those that govern evaporation rate. The maximum evaporation rates, within which the adults of various species carry on their normal activities, vary rather widely but even for *Tipula oxytona, Brachypremna dispellens, Limonia liberta* and *Helobia hybrida,* which appear to tolerate the highest evaporation rates of any Florida crane-flies, the maximum hardly exceeds 1.5 ml. per hour as measured with a standard Livingstone black, spherical atmometer, and for most of the species it is markedly less than this.

The factors that determine evaporation rate are chiefly relative humidity, air movement, and insolation. These vary widely and independently of one another and the behavior of the adult crane-fly is affected by changes or gradients in any one of them. Most of the adults are described as crepuscular or nocturnal in the annotated list (pages 44-61) but this habit is, at least in part, due to the fact that outside of their shaded daytime haunts, the diurnal evaporation rate is ordinarily high. I have had occasion to observe a number of species in such natural gradients of humidity as are provided by unevenly wetted cliffs and stream banks, and noted that individuals in situations with 95-100% humidity showed much greater toleration of light than those in situations where the humidity was 85-90%,[7] and adults of *Diotrepha mirabilis, Limonia cinctipes, L. distans, L. rara, Epiphragma solatrix* and *Pilaria tenuipes*, crepuscular to nocturnal species, when placed in large cylinders with air of known humidity, were much less negative to bright north light in 98-100% than in 70-75%.

A number of afternoons have been spent in the Devil's Mill Hopper observing the activities of the adults from 2-3 p.m., when the evaporation rate is at its maximum, until dusk. Here the duration of the maximum evaporation rate just above the herb stratum, shows a decided gradient from the bottom to the top of the slopes. By 4:00-4:30 p.m. the relative humidity at the bottom has risen to 90-100% and the black bulb evaporation rate fallen to less than 0.5 ml. per hour. At this time adults of numerous species begin their activities near the bottom of the Mill Hopper. Undisturbed individuals of nearly all species take to the wing or begin to walk actively over exposed portions of rotten logs, tree trunks, and earth and limestone banks; mating and oviposition are frequently observed. Halfway up the slopes, even on the south slopes where the light was equally reduced, the humidity above the herbage stratum was still low, 55-65% and except in small rill gullies and isolated mossy caverns, where the evaporation rate is uniformly low, the crane-flies remained in their sheltered resting places. By 5:00-5:30 p.m. the evaporation rates on the middle slopes were rapidly decreasing and the crane-flies here emerged from their sheltered retreats and flew about, above the herbage stratum. At the top of the Mill Hopper, the same species were not on the wing until late dusk, 7:00-7:30 p.m.

During February, March, April, November and December, when adults of the majority of the species are most abundant, many types of general habitats do not provide retreats with sufficiently low diurnal evaporation rates. Numerous individuals that invade such habitats at times of generally prevalent low evaporation rates (still, overcast days and humid nights) are often trapped by the return of normal daytime conditions and seeking shelter in near-by but insufficiently protected hiding places fail to survive the maximum evaporation rates of mid-afternoon. One can frequently observe such

[7] As determined with rotary psychrometer, within 2-3 inches of face of bank.

a series of events in a flat woods or pecan grove that borders a lake or is near a swamp or marsh. At night, these comparatively dry situations may be invaded by large numbers of recently emerged adults and those that remain until daylight take refuge within leaf clusters, crevices in bark, between exposed roots, and in the comparatively xeric herbage. Here they are cut off by the rapidly increasing evaporation rate and may be picked up with forceps or fingers, apparently too feeble to move. On one clear, sunny day in June, I placed gauze bags around several clumps of pecan leaves in which specimens of *Helius flavipes* were resting and from which they could hardly be flushed, into the dry surrounding air, at 10:00 a.m. By 4:00 p.m. five out of seven were dead.

Too low an evaporation rate, or markedly low rates for prolonged periods do not appear to form seriously limiting factors and, ordinarily, can be avoided by moving through very short distances. Emerging and teneral adults occasionally show a high mortality rate in exceptionally wet weather but at these times the low evaporation rates prevail throughout all types of habitats. A number of crane-flies do not occur in the wettest types of habitats but their absence appears to be correlated with specific habitat requirements of the immature stages.

Habitat Requirements of the Immature Stages

The needs of the comparatively long-lived larval stage are more specific and complex than those of the adult. The larvae have small powers of locomotion, need a much longer time to complete their development, and have specific and, for most species, precise requirements for moisture and food. The adaptations of the larvae for respiration and locomotion are also often limiting factors. Those species with more or less truly aquatic larvae (*Tipula abdominalis, T. caloptera,* the first instar of several species of Tipula of the *tricolor* group, Eriocera, *Limonia canadensis,* and others) require well aerated water. The larvae of *Ptychoptera rufocincta* and *Bittacomorpha clavipes* are independent of dissolved oxygen but require a supporting stratum within 30-40 millimeters of the surface. Most of the more or less amphibious larvae that inhabit semi-suspended silt are chiefly depending upon aerial respiration and unable to endure prolonged submergence. Many of these larvae bear, on the ventral margins of their caudal disks, long tufts or fans of un-wettable hairs, which, when pulled down into the silt, form a minute tube some 10-15 millimeters long, that enables the submerged larvae to maintain aerial contact with the surface, or, if drawn entirely beneath the surface, entrap a bubble of air and hold it in contact with the stigmata. The ability to form such air tubes or entrapped bubbles is limited by the wetness of the medium and the fineness of its particles. Larvae that live well beneath the surface in damp soil, wet sand or rotten wood utilize the soil (or wood)

atmosphere and when their habitat is flooded for prolonged intervals are forced to bring at least their caudal disks into contact with an air surface.

The habitable area may be very small. A patch of algae, mosses or liverworts a few inches square, a somewhat larger expanse of mud or silt, two or three square feet of properly conditioned soil, or a few cubic inches of wood in the proper stage of decay often is sufficient. For many species the specific habitat is dependent upon the coincidence of several variable details that may be provided by outwardly dissimilar major habitats. For these species the larval habitat is not the recognizable and typical complex of topography, soil, drainage and vegetation but a more or less local and minor part of it, and such correlation as exists is due to the fact that certain larval habitats are somewhat regularly provided by certain types of major habitats, occasionally or exceptionally by others, and practically never by still other types. The larval habitats of *Diotrepha mirabilis, Epiphragma solatrix, Atarba picticornis* and *Elephantomyia westwoodi* are hardwood logs in certain stages of sodden decay. A hardwood swamp or low hammock most typically maintains supplies of dead wood in contact with sufficiently wet earth; seepage areas and stream margins provide the requisite soil moisture but may be deficient in dead wood; mesophytic hammocks are apt to lack the requisite permanent soil moisture; and high hammocks and pine woods are invariably deficient in one or both requisites.

Species in which the larvae require saturated earth are dependent upon a water supply that will not vary beyond tolerated limits and earth of the proper composition, texture and reaction. Spots or zones where the proper type of soil is coincident with the requisite moisture are typical of certain types of major habitats and only rarely or exceptionally provided by others. The larvae of *Polymera georgiana* occur in somewhat more than saturated deposits of fine, black, organic silt and are typically found about the edges of sink-hole ponds, but they may also be taken from the margins of larger ponds and lakes where cattle tracks, or other small depressions along the wet shore line, allow the accumulation of the light, fine silt.

Other species have a much closer correlation with definite types of major habitats. *Tipula abdominalis* is restricted to small sand bottomed streams and occurs in nearly all of them; several species of Tipula, whose larvae live in the soil of mesophytic hammocks, are definitely correlated with this major habitat; and the majority of flatwoods and bay inhabitants are restricted to these distinct types of northern Florida conditions.

Except for species with aquatic or semi-aquatic larvae, the pupal habitat is usually provided by the situation in which the larvae exist. For nearly all aquatic species a separate pupal habitat that is accessible to the aquatic larvae and permits the pupae to obtain aerial respiration must be available. For larvae that inhabit the bottom of streams, the pupal habitat is usually found

in the moist earth at the margin and larvae that inhabit submerged moss or algae require that a portion of this vegetation extend to or beyond the water-line.

Comparative Importance of Adult and Immature Habitats in Limiting Local Occurrence of the Species

In most instances it is the presence or absence of a suitable larval habitat that determines whether a species can maintain itself in a given area. The more precise and long-enduring larval habitat required by the majority of species is usually more local and restricted than a suitable habitat for the adult, for the needs of the latter for high humidity and shade may be furnished by a variety of conditions. Among the numerous species with a habitat distribution chiefly limited by the needs of the immature stages are *Gnophomyia luctuosa* with larvae and pupae that live in the rotting heartwood of living trees, *Pseudolimnophila contempta, Polymera rogersiana* and *Gonomyia slossonae* in which the larvae are apparently restricted to definitely basic seepage areas, and *Tricyphona inconstans* with immature stages that are intolerant of high temperatures and, in Florida, are restricted to seepage areas in which there is a considerable flow of soil water.

The Size of the Major Habitat

The extent of the area occupied by a given type of major habitat is chiefly of importance as it affects the unbroken continuance of the specific habitats contained within it. The numerous species with larvae that inhabit rotten wood, or the mosses and fungi growing upon it, are dependent on a definite stage in a comparatively rapid succession. The length of time that a given species can find a larval habitat within a single piece of dead wood will depend upon the size of the log or branch, the rate of decay, and the stage or stages that are inhabited by the species in question. In more than a score of logs and branches in which the rate of decay and the crane-fly population have been carefully followed from year to year, the maximum time that a single log was inhabited by the same species has been four years and for many of the smaller branches a proper stage of decay does not last for more than one or two generations of larvae.

When the major habitat is extensive new supplies of dead wood are constantly entering the decay succession. As a consequence emerging adults find suitable places for ovipositing within the normal limits of their habitat, and the species maintains itself as a continuous inhabitant of that area. When the supply of dead wood is limited or sporadic, as it often is in a small extent of hammock or swamp, the chance that adults will emerge within that habitat are decreased or, if the adults do emerge, the chances that they will find wood in a suitable stage for ovipositing are less, and sooner or later the species is apt to disappear from the isolated small habitat. From time to time such

small areas are repopulated by adults that wander in during periods of generally low evaporation rates and the species may maintain itself until another break in the supply of wood in the proper stage of decay causes it again to disappear from the small local habitat.

The occasional severe and greatly prolonged dry seasons have their greatest effect on the smaller areas of hammock, swamp and marsh and cause a number of the smaller streams and seepage areas to completely disappear. At these times many of the smaller, isolated areas of mesophytic vegetation are severely dessicated, and sometimes swept by severe ground fires that destroy all leaf mould and rotten wood, while in the larger hammocks and swamps both severe dessication and fires tend to be limited to the marginal areas.

HABITAT DISTRIBUTION

The distribution of the crane-flies of northern Florida by major habitats is given in Table V and supplemented in the Annotated List. In the former, only records from northern Florida are included; in the latter, data from other regions has been drawn upon for a few species that are rare in northern Florida. The numbered order of the species is the same in Table V and the Annotated List.

EXPLANATION OF ABBREVIATIONS AND SYMBOLS IN TABLE V

NUMBER OF TIMES RECORDED—Number of separate instances in which adults or immatures has been recorded with definite habitat data. Numbers followed by a plus sign (+) are conservative minima.

DISTRIBUTION—C-1, coastal plain, north to New England; C-2, coastal plain, north to New Jersey or Washington, D. C.; C-3, coastal plain of Florida, Georgia and South Carolina, in some instances, west along Gulf Coastal Plain to Louisiana; Cos., cosmopolitan species.

F-1, limited to northwestern Florida; F-2, northern Florida, south to northern Volusia, Marion and Levy counties; F-3, northern and central Florida, south to Orange and Manatee counties; F-4, throughout Florida; F-5, southern Florida, north to Alachua and Levy counties; Fn, endemic species with northern relationships; Fs, endemic species with neotropical relationships.

N-1, eastern North America, north to New England, Canada and northern Michigan; N-2, eastern North America, north to lowland New York, Pennsylvania and southern Michigan; N-3, eastern North America, north to District of Columbia and southern Indiana.

S, neotropical species (in some cases, extending northward to southern Indiana).

MAJOR HABITATS—1, Juncus Marshes, coastal tidal flats; 2a, shaded seepage areas and small rills; 2b, rocky seepage areas, wet cliffs, etc.; 3a, wooded rill and brook courses, usually in ravine or valley; 3b, open, grassy rill and brook courses; 4a, swamp streams; 4b, bog streams; 5, larger calcareous streams; 7, fluctuating ponds; 8, sink-hole ponds; 9, lake, pond and marsh shore-lines; 10a, "Prairies," marshes characterized by floating and submerged vegetation; 10b, marshes dominated by emergent vegetation; 11a, cypress-ponds and "bays"; 11b, cypress ponds of lake shores and flood plains; 11c, hardwood and mixed swamps of lake shores and flood plains; 12, low hammocks; 13, mesophytic hammocks; 14, high hammocks; 15a, grassy flatwoods; 15b, palmetto or hard-pan flatwoods; 16, "High-Pine" lands, more particularly the somewhat atypical high pine of Blanton and similar soils.

A, Devil's Mill Hopper, Alachua County; B, "Torreya" Ravines of Apalachicola River bluffs; C, Red Clay Hills of Jackson, Jefferson and Leon counties; D, Ash and Gum Swamps of Jackson County.

TABLE V. *Distribution of crane-flies of northern Florida by major habitats.*

Species	Number of Times Recorded		Distribution		Typical Habitats	
	Adts.	Imms.	Geog.	Fla.		
1. P. rufocincta	28	12	N-1	F-2	4b 11a	D
2. B. clavipes	100+	100+	N-1	F-3	3a 3b 4a 10b 11b	A B C D
3. T. abdominalis	27	100+	N-1	F-2	3a	A B
4. T. caloptera	100+	100+	N-1	F-2	5 2b 3a	A B
5. T. duplex	50+	8	N-1	F-2	13 (12+14)	B C
6. T. eluta	12	0	N-1	F-2	3a (3b)	A B
7. T. flavoumbrosa	37	3	N-2	F-2	14 13	C
8. T. floridensis	15	0	C-3	F-2	3a	B
9. T. fraterna	18	0	N-2	F-2	3a	A B
10. T. furca	100+	100+	N-1	F-3	3a 3b 2a (9)	A B D
11. T. hermannia	3	0	N-1	F-1		B
12. T. jacobus	5	1	N-2	F-2	10b 15a (3b)	
13. T. ludoviciana	23	4	C-3	F-4	15a	
14. T. mallochi	4	0	N-1	F-1		B C
15. T. manhatta	2	1	N-2	F-2?	10b	
16. T. oropezoides	3	1	N-1	F-1		B
17. T. osceola	10	2	Fn	F-2?	11a 15a	
18. T. oxytona	100+	30+	Fn	F-2	16 14	
19. T. sayi	2	0	N-1	F-1	10b	
20. T. subeluta	12	1	C-2	F-2	11c	
21. T. synchroa	36	20	Fn	F-2?	2a 3a	A
22. T. tricolor	100+	75+	N-1	F-3	3a 2a 3b 5 (9)	A B C D
23. T. triplex	50+	3	N-1	F-2	12 13 11c	B C
24. T. ultima	2	0	N-1	F-1	10b	
25. T. unifasciata	2	0	N-1	F-1	14 ?	C
26. Tipula sp. (no. 1)	1	1	Fn	??	12	
27. Tipula sp. (no. 2)	2	1	Fn	??	11a	
28. N. incurva	5	0	N-1	F-1	13	B C
29. N. macrocera	35	0	N-1	F-2	3a 11c 12	A B C
30. N. okefenoke	100+	0	C-3	F-3	11c 3a 12 4a	C D
31. N. suturalis	100+	14	C-3	F-4	3b 12 13 9 10b	C D
32. N. virescens	17	0	N-2	F-2	13 9	C
33. O. albipes	25	0	N-1	F-1	3a	B C
34. O. dorsalis rogersi	17	0	N-2	F-1	3a 11c 4a?	B C
35. O. obscura	75+	12	N-1	F-2	13 12	A B C
36. O. sayi	4	2	N-1	F-2?		A
37. O. subalbipes	100+	20+	N-2	F-2	3a 3b (4a 4b)	A B C D
38. D. dispellans	100+	0	S	F-4	12 13 14 3a 11c 15a	A B C D
39. M. longipennis	18	0	S	F-5	3b 3a	
40. D. mirabilis	30	100+	S	F-4?	3a 11c 2a 12	A B C D
41. D. australis	15	0	N-3	F-2	14 13	C
42. D. megaphallus	3	1	N-3	F-1	14	C
43. D. rogersi	1	0	Fn		13 ?	
44. D. sobrina	4	0	N-2	F-1	14 13	C
45. D. winnemana	50+	3	N-2	F-2	13	C
46. H. flavipes	100+	2	N-1	F-3	10b 9 3b	
47. L. cinctipes	4	15	N-1	F-2	3a (11c)	A B
48. L. immatura	2	0	N-1	F-1		D
49. L. macateei	3	2	N-2	F-1		B
50. L. rara	50+	12	N-2	F-2	3a 11c 12	A B
51. L. rogersiana	3	0	Fs	F-2	3a ?	B
52. L. subapicata	2	1	Fs	??	12 ? 13 ?	
53. L. brevivena	16	0	N-2?	F-4	3b 15a	
54. L. distans	100+	35+	C-3	F-4	10a 7 9 10b	
55. L. divisa	50+	3	N-1	F-2	3a 2a 11c 12	A B D
56. L. floridana	12	5	C-3	F-3?	1	

TABLE V. *(Continued)*

Species	Number of Times Recorded		Distribution		Typical Habitats	
	Adts.	Imms.	Geog.	Fla.		
57. L. liberta	50+	0	N-1	F-2	3b 9 10b 15a	C
58. L. bryanti	4	0	N-1	F-2	3a 13	B
59. L. domestica	100+	0	N-1	F-4	13 11c 3a 12	A B C D
60. L. fidelis	2	0	N-2	F-1		B
61. L. shannoni	75+	0	N-3	F-3	13 3a 11c	A B C
62. L. schwarzi	14	0	S	F-5	3a 3b	A
63. L. canadensis	28	7	N-1	F-3	5 2b (3a)	A
64. L. distincta	2	0	N-2	F-2?	3a ?	
65. L. rostrata	100+	75+	N-1	F-3	2b 3a 3b 11c	A B D
66. L. vanduzeei	34	3	Fs	F-5	15a 11a	
67. L. virescens	8	0	S	F-5	3b	
68. E. fascipennis	2	0	N-1	F-1		D
69. E. solatrix	100+	100+	N-2	F-3	11c 3a 12 11a	A B C D
70. P. australina	50+	6	N-3	F-2	4a 11c 2a	A B
71. P. contempta	100+	100+	N-2	F-3	2a 3a	A B
72. P. luteipennis	100+	100+	N-1	F-3	10b 4a 3a 3b 8 9 11a	A B C D
73. L. fuscovaria	50+	3	N-1	F-2	2a 3a	A B D
74. L. macrocera suffusa	100+	32	C-3	F-2	3a 4a?? 2a	A B D
75. L. irrorata	3	0	C-2	F-1	11c 12	D
76. L. marchandi	3	0	C-2	F-2	3a	B
77. L. epimicta	27	0	Fn	F-3	11c (3a 11a)	D
78. L. osceola	50+	0	Fn	F-2	11a 15a	
79. P. georgiae	50+	20+	C-3	F-4	8 9 (4a 11b)	A B
80. P. rogersiana	18	15	Fs	F??	2a	A
81. P. arguta	50+	3	Fn	F-2	11a 4a 11b 11c	
82. P. quadrata	4	2	N-1	F-1	11c 12	D
83. P. recondita	10	6	N-1	F-2	4a 3a 2a	A B C
84. P. tenuipes	100+	25+	N-1	F-3	3a 2a	A B C D
85. U. rogersella	3	0	N-2?	F-1	11c 12	D
86. E. fuliginosa	0	3	N-2	F-2?	3a 3b	A
87. P. albitarsis	14	2	N-2	F-1	11c 12	D
88. A. picticornis	100+	50+	N-2	F-2	13 12 3a 2a	A B C D
89. T. inconstans	50+	31	N-1	F-2	2a 3b	A B D
90. A. pleuralis	2	0	N-2	F-1	2a	B
91. G. luctuosa	50+	16	N-3	F-3	13 12 11c	A B C D
92. G. tristissima	16	1	N-1	F-1	3a 13	B C
93. T. carolinensis	0	0	C-3?	F-3?	See annotated list	
94. T. complexa	100+	100+	N-2	F-2	13 (12)	A B C
95. T. lucida	75+	0	N-3	F-2	13 3a	A C
96. G. blanda	3	0	N-1	F-1	3b	
97. G. manca	100+	2	N-2	F-4	2a 3a 3b	A B C D
98. G. pleuralis	100+	4	S	F-4	7 11a 11b 11c	B D
99. G. puer	75+	2	S	F-4	11a 15a 3a	A
100. G. slossonae	24	13	S	F-4	2a 3a	A
101. G. subcinerea	8	0	N-1	F-2	2a 3a	A B
102. G. sulphurella	100+	50+	N-1	F-4	3b 3a 2a 9	A B C D
103. O. brevicalcarata	1	0	N-2?	F-1		B
104. O. nigrapila	14	1	N-2	F-2	2a (3a)	A B C
105. E. osceola	18	2	Fn	F-2	3a	A B
106. E. seminole	6	1	Fn	F-2	4b 11a-("bays" only)	
107. E. septemtrionis	11	0	N-1	F-1		B
108. E. subchlorophylla	26	4	C-2	F-2	4a 11c	
109. E. vespertina	50+	50+	N-1	F-2	8 9 10b 3a 2a 11c	D
110. E. noctivagans	15	0	C-2	F-2?	3b 15b?	
111. E. caloptera	100+	20+	N-1	F-3	3a 2a 11c 12 9	A B C D
112. E. needhami	100+	9	N-1	F-2	2a 3a 3b	A B
113. E. parva	100+	0	N-1	F-4	9 2a 3b 3a 11c	A B C D

TABLE V. (*Continued*)

Species	Number of Times Recorded		Distribution		Typical Habitats	
	Adts.	Imms.	Geog.	Fla.		
114. E. sp. close to knabi.	4	0	Fs?	F-5?	3b 15	
115. E. graphica.........	7	0	N-2	F-2	2a 3a	A B C
116. E. venusta.........	9	2	N-1	F-1	3b 2a	B D
117. M. floridensis.......	43	3	Fn	F-2	3a 2a	A B C
118. M. forcipulus.......	100+	8	N-1	F-2	2a 3a	A B C D
119. M. pubipennis......	5	0	N-1	F-1		B
120. M. sp., hirtipennis group.........	50+	6	??	F-2	2a 3a	A B C
121. D. niphadias........	7	0	N-2	F-1	3a 2a	B
122. H. hybrida.........	28	0	Cos.	F-3	3b 15a	C
123. T. anomola.........	2	0	Cos.	F-4	10b	
124. E. westwoodi.......	50+	50+	N-1	F-2?	13 12 11c 3a 2a	A B C D
125. T. magna..........	100+	0	C-2	F-4	11c 10b 11b 11a 4a	A D

ANNOTATED LIST OF SPECIES

FAMILY PTYCHOPTERIDAE

1. *Ptychoptera rufocincta* Osten Sacken.

Adult: Diurnal within shaded herb and shrub strata; sphagnum pools of hardwood swamps and "bays." Oviposition into sphagnum at water line.

Immature Stages: 15-30 mm. below surface in sphagnum and plant debris, stagnant or slowly seeping, acid water (pH 4.0-5.6); respiration aerial by slender, elongate caudal (larva) or pronotal (pupa) breathing tube; larvae feed upon living sphagnum and plant debris.

2. *Bittacomorpha clavipes* (Fabricius).

Adult: Diurnal in shaded or partially open areas; hardwood swamps, marshes and sluggish, small streams. Oviposition while in flight by dipping tip of abdomen into water of larval habitat; 3-5 eggs deposited at a time.

Immature stages: Among plant debris of semi-stagnant water, swampy or marshy pools of rills and brooks; older larvae require support within breathing-tube-reach (15-30 mm.) of surface; pupae able to wriggle to surface and hang suspended by tip of pronotal breathing horn; the flocculent, reddish or black debris ingested by larvae has rich flora of algae and bacteria.

FAMILY TIPULIDAE

Subfamily Tipulinae

3. *Tipula abdominalis* (Say).

Adult: crepuscular or nocturnal; daytime habitat, shaded boles of trees and beneath leaves of taller shrubs, along wooded streams. Oviposition into sandy margins of rills and brooks.

Immature stages: larvae among leaf drift and matted rootlets of sand-bottom streams or in sand of stream bottom; respiration wholly aquatic when in well aerated water, otherwise aerial by means of caudal stigmata; feeds upon leaf drift and attached filamentous algae and diatoms; pupation in damp sand or sandy loam of stream margin, well above water line.

4. *Tipula caloptera* Loew.

Adult: largely crepuscular or nocturnal; daytime habitat, among shrubbery of stream banks. Oviposition into algal and moss mats on wet rocks or hard earth banks, usually a few mm. below the water line.

Immature stages: wet or submerged mats of mosses and algae; larvae can live for months wholly submerged in well aerated streams; pupation takes place above water line, in tunnels in wet or damp mosses, or in floating mats of algae; larvae feed on living mosses and algae.

5. *Tipula duplex* Walker.

Adult: crepuscular to diurnal; mesophytic hammocks. Oviposition into damp but friable soil of hammock floor, usually in vicinity of dead wood.

Immature stages: in moist, friable soil beneath leaf mould or slightly sunken dead wood.

6. *Tipula eluta* Loew.

Adult: crepuscular or nocturnal; daytime habitat, the herb and shrub strata of stream banks and ravines.

Immature stages: unknown; almost certainly aquatic or semiaquatic in brooks and rills.

7. *Tipula flavoumbrosa* Alexander.

Adult: somewhat diurnal to crepuscular; high and mesophytic hammocks.

Immature stages: sandy loam of hammock floor, among roots of grasses and herbage.

8. *Tipula floridensis* Alexander.

Adult: markedly crepuscular or nocturnal; daytime habitat, overhung, moist banks of streams.

Immature stages: unknown; probably similar to *T. caloptera*.

9. *Tipula fraterna* Loew.

Adult: crepuscular and nocturnal; daytime habitat, herbage of shaded stream banks.

Immature stages: unknown; probably aquatic or semiaquatic in rills and brooks.

10. *Tipula furca* Walker.

Adult: chiefly crepuscular; daytime habitat, herbage and low shrubbery of shaded or open streams. Oviposition into saturated silt or sandy silt, margins of rills and brooks.

Immature stages: larvae aquatic or semiaquatic when young, semiaquatic in later instars; feed on plant debris, probably for its microscopic flora; pupation in wet earth or beneath moss clumps, above water line.

11. *Tipula hermmania* Alexander.

Adult: crepuscular; daytime habitat, on cool, shaded banks and rocks, ravines and deep woods. The only Florida records are for the Torreya Ravines of Liberty County.

Immature stages; unknown.

12. *Tipula jacobus* Alexander.

Adult: crepuscular to somewhat diurnal; marshy and open-swamp streams.

Immature stages: saturated or wet soil among grass tussocks of marshy streams.

13. *Tipula ludoviciana* Alexander.

Adult: crepuscular to diurnal; low grassy flatwoods (in southern Florida, often abundant in the grassy "glades"). Oviposition into wet soil among rank growths of grasses and herbs.

Immature stages: wet, semi-plastic soil of low flatwoods; larvae feed or roots of grasses and sedges.

14. *Tipula mallochi* Alexander.

Adult: largely crepuscular; mesophytic hardwood formations; all Florida records from partially deciduous hardwoods ravines of western Florida; daytime habitat, upper or under side of leaves of shrubs and lower trees.

Immature stages: (Indiana) soil of forest floor, just below leaf mould.

15. *Tipula manhatta* Alexander.

Adult: crepuscular or nocturnal; grass and shrub marshes; daytime habitat, within grass and sedge clumps.

Immature stages: wet, rather plastic soil between grass hummocks.

16. *Tipula oropezoides* Johnson.

Adult: crepuscular to nocturnal; daytime habitat, mossy crevices in banks, etc.; known in Florida only from deep mesophytic Torreya Ravines of Liberty County.

Immature stages: moist to wet clumps of moss, on wet rocks, stream banks and roots.

17. *Tipula osceola* Alexander.

Adult: Diurnal to crepuscular; low grassy margins between flatwoods and cypress ponds or bays. Oviposition into sphagnum covered black soil of adult habitat.

Immature stages: semi-plastic, acid soil of low grassy flatwoods and cypress pond margins.

18. *Tipula oxytona* Alexander.

Adult: diurnal to crepuscular; wire-grass grown, high pine forests and high hammocks of Blanton soils. Oviposition into sandy soil at edges of wire-grass clumps.

Immature stages: friable sandy soil, usually within 50 mm. of surface but as deep as 200 mm. in dry seasons; larvae feed on rootlets of wire grass.

19. *Tipula sayi* Alexander.

Adult: Chiefly crepuscular; marshy or shrub-swamp situations. All Florida records from northwestern portion of state.

Immature stages: wet plastic soils of grass and sedge marshes.

20. *Tipula subeluta* Johnson.

Adult: crepuscular to nocturnal; daytime habitat, herb and shrub strata, mixed and hardwood swamps of lake shores and flood plains.

Immature stages: semi-aquatic, margins of silty pools and muddy lake shores.

21. *Tipula synchroa* Alexander.

Adult: chiefly nocturnal; deeply shaded seepage areas and wet shaded stream banks; daytime habitat, deep within rank growths of ferns and other herbage.

Immature stages: wet, black, organic silt of seepage areas.

22. *Tipula tricolor* Fabricius.

Adult: crepuscular to slightly diurnal; wet shaded situations. Oviposition into saturated or barely submerged sandy soil of rill and brook margins.

Immature stages: larvae aquatic or semi-aquatic in leaf drift and sandy margins of rills and brooks; pupae in wet sand or sandy soil, above water line.

23. *Tipula triplex* Walker.

Adult: crepuscular to diurnal; low and mesophytic hammocks; daytime habitat, leaves of taller shrub and tree strata.

Immature stages: damp to wet surface soil of low wooded areas, usually flood plains or lake shores.

24. *Tipula ultima* Loew.

Adult: chiefly crepuscular; daytime habitat, among rank grasses and sedges of marshy situations.

Immature stages: wet or saturated, plastic soil of marshy situations.

25. *Tipula unifasciata* (Loew).

Adult: at least partially diurnal; rather open, dry, mesophytic hillside woods of western Florida.

Immature stages: unknown.

26. *Tipula* sp. number 1.

Taken only once, but then in large numbers; adults on the wing, the males in search of females, in a deeply-shaded, river flood-plain, low hammock. Two mature larvae and a few pupae were found near the surface, in the moist, plastic soil of the hammock.

27. *Tipula* sp. number 2.

Adult: crepuscular; daytime habitat among tall grasses and sedges of cypress pond margin, grassy flat woods.

Immature stages: larvae unknown; pupae in rather dry, plastic soil between sedge hummocks of adult habitat.

28. *Nephrotoma incurva* (Loew).

Adult: crepuscular or nocturnal; the few Florida records (northwestern Florida) are from deep shaded ravines or low hammocks.

Immature stages: unknown.

29. *Nephrotoma macrocera* (Say).

Adult: diurnal to crepuscular; moist hammocks in vicinity of streams.

Immature stages: wet to saturated silt, rill margins and marshes.

30. *Nephrotoma okefenoke* (Alexander).

Adult: crepuscular to somewhat diurnal; herbage and low shrubbery of swampy situations.

Immature stages: unknown but teneral adults obtained in tent trap in shaded, brook-margin seepage-area.

31. *Nephrotoma suturalis* (Loew).

Adult: crepuscular or nocturnal; herbage and low shrubbery, open grassy hammocks and creek margins. Oviposition into bare spots in damp, friable soil.

Immature stages: wet to moderately damp, sandy soils; larvae feed on grass rootlets. Larvae and pupae were taken in numbers from cabbage plots where clean cultivation had been carried on for at least four weeks.

32. *Nephrotoma virescens* (Loew).

Adult: chiefly crepuscular; shrub stratum of mesophytic and low hammocks.

Immature stages: unknown.

33. *Oropeza albipes* Johnson.

Adult: chiefly crepuscular; daytime habitat, moist recesses beneath overhanging banks and within rank herbage, shaded stream banks. Oviposition into wet mosses of shaded stream banks.

Immature stages: unknown.

34. *Oropeza dorsalis rogersi* Alexander.

Adult: crepuscular or nocturnal; rank herbage of swampy or marshy rills. All Florida records for Jackson and Liberty counties.

Immature stages: unknown; probably in wet mosses.

35. *Oropeza obscura* Johnson.

Adult: nocturnal; daytime habitat, within hollow trees and dark, cool recesses of banks and cliffs. Oviposition into moss clumps, on logs, roots and boles of living trees, or on wet, shaded, earth banks.

Immature stages: wet to moderately dry moss clumps; pupation in short tunnels between moss and wood; larvae feed on surface of moss, at night.

36. *Oropeza sayi* Johnson.

Adult: nocturnal; daytime habitat, rank herbage of wet shaded soil.

Immature stages: wet mosses on sodden, shaded logs.

37. *Oropeza subalbipes* Johnson.

Adult: crepuscular; daytime habitat, beneath luxuriant ferns and herbage that overhang wooded rills and small brooks. Oviposition into mats of mosses or liverworts, wet shaded rill banks.

Immature stages: saturated mosses and liverworts, on wet earth banks, on rocks and (more rarely) sodden logs; larvae feed on growing portion of liverworts and mosses, mainly at night.

38. *Brachypremna dispellans* (Walker).

Adult: crepuscular to diurnal; herbage and shrub strata of nearly all types of hammocks, moist flatwoods and swamps.

Immature stages: unknown.

39. *Megistocera longipes* (Macquart).

Adult: crepuscular to slightly diurnal; closely confined to banks of small hammock brooks, where groups of adults rest on leaves of *Saururus* or on the mossy banks.

Immature states: unknown.

Subfamily Limoniinae

40. *Diotrepha mirabilis* Osten Sacken.

Adult: nocturnal to crepuscular; daytime habitat, underside of leaves and fronds, deeply shaded situations where evaporation rate is nearly zero. Oviposition into soft, bare areas of sodden, rotten wood.

Immature stages: rotten logs, branches and twigs, in such a stage of decay that the soft annual rings flake off with slight pressure; larvae feed principally on the micro-flora of these wet logs, blue-green algae and fungi.

41. *Dicranoptycha australis* Alexander.

Adult: crepuscular to diurnal; herbage and shrub strata of moderately open, grassy mesophytic woods and hammocks.

42. *Dicranoptycha megaphallus* Alexander.

Adult: largely diurnal, but continuing their activities until after dusk; herb and shrub strata of high hammocks and upland woods; more frequent in clay hill woods of western Florida.

Immature stages: moderately dry, plastic soil of well drained woods; pupation in a thick-walled earthen cell that offers considerable resistance to dessication.

43. *Dicranoptycha rogersi* Alexander.

Adult: a single record; abundant and active in mid-afternoon among the herbage of an extensive, well-drained, mesophytic hammock.

Immature stages: unknown.

44. *Dicranoptycha sobrina* Osten Sacken.

Adult: diurnal to crepuscular; herbage and low shrubbery of open, grassy, mesophytic hammocks and upland woods.

Immature stages: moderately moist, rather friable soil of open woods.

45. *Dicranoptycha winnemana* Alexander.

Adult: diurnal; herb and shrub strata, well drained mesophytic hammocks of lake shores. A distinctly more mesophytic type of habitat than occupied by *D. australis, megaphallus* or *sobrina* but always in well drained hammocks on Norfolk soils.

Immature stages: moist, friable surface soil of adult habitat, beneath leaf mould; larvae feed on rootlets of herbage; pupation in earthen cell that is less compact and more fragile than that of *D. megaphallus.*

46. *Helius flavipes* (Macquart).

Adult: crepuscular; daytime habitat, grass and sedge stratum, marshes, slightly shaded lake margins, and open swamps.

Immature stages: saturated silt and silty sand, grass and sedge grown margins of marshes and lakes.

47. *Limonia cinctipes* Say.

Adult: crepuscular or nocturnal; daytime habitat, on shaded mossy stumps, logs or boles, often beneath loose slabs of bark.

Immature stages: in fleshy fungi on wet rotten logs and stumps—mainly Poria or Polyporus—either in the body of the fungus or the mycelia-filled wood at its base; larvae feed on tissues of the fungus.

48. *Limonia immatura* Osten Sacken.

The few Florida records for this species are all for Jackson County in the northwestern corner of the area studied. The immature stages are unknown but the habits of the adult appear quite like those of *L. cinctipes* to which *L. immatura* is very closely related.

49. *Limonia macateei* (Alexander).

Adult: diurnal to crepuscular; usually in the immediate vicinity of damp, fungus-grown logs and stumps in moist, shaded ravines and valleys. Oviposition into fungi or moist, mycelia-filled wood and bark.

Immature stages: fungi—Polyporus, Fomes, Poria—on wet rotting wood or in the cavities of logs and stumps; larvae feed on soft, often semi-fluid tissues of fungi; pupation in drier upper portion of the fungus or in loose bark at its base.

50. *Limonia rara* (Osten Sacken).

Adult: crepuscular or nocturnal; daytime habitat, beneath loose bark, in crevices between exposed roots, etc., damp shaded situations.

Immature stages: in sodden, mycelia-riddled logs or in fleshy fungi growing on wet, rotten wood.

51. *Limonia rogersiana* (Alexander).

Adult: nocturnal or crepuscular; moist, shaded, stream valleys and ravines.

Immature stages: unknown.

52. *Limonia subapicata* Alexander.

Adult: crepuscular or nocturnal; low and mesophytic hammocks.

Immature stages: about a hundred larvae were taken from beneath loose bark of a large *Pinus glabra,* fallen about 12 months before. Here the larvae occurred in the damp woodpowder between bark and sapwood. The alimentary tracts of the larvae were filled with this black woodpowder.

53. *Limonia (Dicranomyia) brevivena* (Osten Sacken).

Adult: chiefly crepuscular; among grasses of marshy rills, cypress-pond margins, and flatwoods.

Immature stages: unknown. Several adults emerged from a quantity of thin sphagnum and other mosses gathered from the floor of grassy cypress-pond margins.

54. *Limonia (Dicranomyia) distans* (Osten Sacken).

Adult: chiefly crepuscular or nocturnal; within grass and sedge stratum, margins of "Prairies," marshy lakes and ponds. Oviposition into floating films of algae, the female standing either on the algal film or on the stalks of emergent vegetations.

Immature stages: in floating films or thin mats of green algae, among emergent or floating water plants, "Prairies" and margins of shallow ponds and lakes; larvae feed on living filaments of algae; larval respiration chiefly aerial; pupae project from surface of algae at mouths of gelatinous larval tubes.

55. *Limonia (Dicranomyia) divisa* Alexander.

Adult: crepuscular or nocturnal; damp shaded situations.

Immature stages: damp to wet mosses, often scanty films, on sodden wood, or exposed roots of swamp and stream-side trees.

56. *Limonia (Dicranomyia) floridana* (Osten Sacken).

Adult: diurnal and crepuscular; during daytime within *Juncus* stratum of tidal flats. Oviposition at low tide, into algal tufts and films, on floor of tidal flat.

Immature stages: in tough films and tufts of algae about bases of Juncus stems and over floor of tidal flat within the Juncus formation; larvae feed on terminal filaments of algae.

57. *Limonia (Dicranomyia) liberta* (Osten Sacken).

Adult: crepuscular; among grasses and sedges, open or partially shaded, moist situations.

Immature stages: unknown.

58. *Limonia (Rhipidia) bryanti* (Johnson).

Adult: largely nocturnal; mesophytic hammocks and moist, shaded ravines.

Immature stages: never taken in Florida. Alexander (1920) records larvae and pupae beneath bark of moist, decaying wood.

59. *Limonia (Rhipidia) domestica* (Osten Sacken).

Adult: crepuscular or nocturnal; daytime habitat, herbage and shrub strata of wide variety of wooded situations.

Immature stages: unknown. (Reported in literature as bred from decaying vegetables and fermented sap of sour-gum).

60. *Limonia (Rhipidia) fidelis* (Osten Sacken).

Adult: largely nocturnal; all Florida records from deep, wooded ravines of Apalachicola River bluffs.

Immature stages: (South Carolina) in damp, powdery material beneath loosened bark of decaying hardwood log.

61. *Limonia (Rhipidia) shannoni* (Alexander).

Adult: crepuscular or nocturnal; herb and shrub strata of mesophytic hammocks, and ravines.

Immature stages: unknown.

62. *Limonia (Rhipidia) schwarzi* (Alexander).

Adult: rare in northern Florida; crepuscular or nocturnal; rank grasses and herbage of damp, shaded or partially shaded situations.

Immature stages: unknown.

63. *Limonia (Geranomyia) canadensis* (Westwood).

Adult: crepuscular, diurnal in humid situations; vicinity of wet rocks, banks and piling, and deep shaded herbage of stream margins. Oviposition into or beneath wet moss and algal films.

Immature stages: saturated or submerged coats of algae and mosses or wet rocks, wet piling, hard stream bottoms; pupation in mouth of gelatinous larval tube, above water line; larvae feed on algae.

64. *Limonia (Geranomyia) distincta* (Doane).

Adult: the two Florida records are both for specimens swept from emergent vegetation, shaded pools of small sluggish streams.

Immature stages: unknown.

65. *Limonia (Geranomyia) rostrata* Say.

Adult: crepuscular to diurnal; damp shaded situations in vicinity of larval habitat; wet rocks, rank herbage and shrubbery. Oviposition into wet mosses or liverworts and algal scum of wet rocks.

Immature stages: leafy liverworts of wet, shaded rill banks; mosses or moss and algal scum beneath or bordering thin trickles on shaded cliffs and rocks; larvae feed on algae, mosses and liverworts. Occasionally taken with larvae of *L. canadensis* but the latter typically in much more aquatic situations.

66. *Limonia (Geranomyia) vanduzeei* (Alexander).

Adult: crepuscular or nocturnal; grass and sedge stratum of low flatwoods; in northern Florida, largely confined to cypress-pond margins.

Immature stages: in scant growths of sphagnum, floor of low, grassy flatwoods.

67. *Limonia (Geranomyia) virescens* (Loew).

Adult: crepuscular to diurnal; among rank grasses and sedges of open or partially shaded, low, wet situations—marshes, grassy flatwoods; frequently abundant in grassy "glades" of south Florida.

Immature stages: unknown.

68. *Epiphragma fascipennis* (Say).

Adult: largely nocturnal; daytime habitat, on damp logs and among herb stratum, wet, mesophytic woods.

Immature stages: apparently identical in habits and habitat with *E. solatrix*. Immatures of both species have been taken from same logs (in Indiana and Tennessee).

69. *Epiphragma solatrix* Osten Sacken.

Adult: chiefly nocturnal; daytime habitat, within herb stratum of moist, shaded woods, often resting on lower sides of moist logs. Oviposition into soft, spongy spots of sodden logs or limbs; old frass-filled burrows of *Passalus cornutus* are frequently utilized.

Immature stages: sodden, often permanently saturated logs and limbs, where the larvae follow old beetle burrows or seams and veins of semi-solid, fungus masses; pupation in mouth of larval burrows; larvae feed on mycelia of fungi and mycelia-riddled wood.

70. *Pseudolimnophila australina* Alexander.

Adult: chiefly crepuscular; rank herbage of swampy rills and seepage areas.

Immature stages: saturated or semi-suspended organic silt, among roots of herbage, seepage areas and margins of swampy rills.

71. *Pseudolimnophila contempta* (Osten Sacken).

Adult: largely crepuscular; among rank herbage in vicinity of larval habitat.

Immature stages: saturated sand-clay or silty sand-clay of rill courses, rill margins, and seepage areas. Largely confined to situations where there is some flow to the soil water and the pH is 7.0-8.5.

72. *Pseudolimnophila luteipennis* (Osten Sacken).

Adult: crepuscular to somewhat diurnal; herbage of marshes and open swamps. Oviposition into deep silt, usually at margin of small pools and shallow water.

Immature stages: saturated or semi-suspended silt, cattail and rush zones of marshes, margins of swamp pools and swamp streams, small mud deposits along sand-bottom streams; the habitat often distinctly acid; larvae are scavengers.

73. *Limnophila fuscovaria* Osten Sacken.

Adult: crepuscular; rank herbage of low hammocks, hardwood swamps and ravines.

Immature stages: saturated silt or sandy silt of shaded seepage areas and stream margins; often common in the saturated, black, organic mud of the gum and ash swamp along Blue Spring Creek (page ....); larvae carnivorous, feeding on small lumbriculid worms and dipterous larvae.

74. *Limnophila macrocera suffusa* Alexander.

Adult: crepuscular to diurnal; herbage and shrubbery of sluggish streams, and swampy seepage areas.

Immature stages: saturated organic silt, often in the thin layer of silt, over sand, margins of sluggish reaches of brooks, swampy seepage areas and muddy rills; pupation in the less saturated margins of such areas; larvae carnivorous.

75. *Limnophila irrorata* Johnson.

Adult: apparently nocturnal; all Florida records from extensive flood-plain hardwood swamps, northwestern Florida.

Immature stages: unknown.

76. *Limnophila marchandi* Alexander.

Adult: crepuscular and nocturnal; all Florida records for bottom of deep, shaded, stream ravines. Oviposition into wet sandy seepage area at margin of brook.

Immature stages: unknown.

77. *Limnophila epimicta* Alexander.

Adult: crepuscular or nocturnal; hardwood and cypress swamps of lake shores and flood-plains.

Immature stages: unknown.

78. *Limnophila osceola* Alexander.

Adult: crepuscular; herbage of cypress ponds, and cypress pond and "bay" margins in flatwoods.

Immature stages: unknown; adults emerged in tent trap over deep, saturated, organic silt, in partially cleared cypress pond.

79. *Polymera georgiae* Alexander.

Adult: chiefly nocturnal; herbage of shaded, or partially open, pond and lake margins.

Immature stages: saturated to semi-suspended fine silt of pond, lake and marsh margins; larvae carnivorous, feeding on small lumbriculid worms.

80. *Polymera rogersiana* Alexander.

Known only from Devil's Mill Hopper, Alachua County, where it is fairly common.

Adult: crepuscular; dense ferns and herbage that border small rill courses.

Immature stages: saturated, plastic sand-clay of seepage areas from disintegrating limestone strata, pH 8.2-8.5; larvae carnivorous, feeding, in part, on larvae of *Erioptera needhami*.

81. *Pilaria arguta* Alexander.

Adult: crepuscular: shaded herbage of swampy situations, particularly the margins of cypress ponds and bays.

Immature stages: saturated organic silt, usually distinctly acid; larvae carnivorous.

82. *Pilaria quadrata* (Osten Sacken).

Adult: crepuscular to diurnal; deeply shaded hardwood swamps of river and creek flood plains, northwestern Florida.

Immature stages: saturated, humus filled soils of hardwood swamps; larvae carnivorous.

83. *Pilaria recondita* (Osten Sacken).

Adult: crepuscular; shaded herbage of swampy streams and seepage areas.

Immature stages: saturated silt of swamp streams and rills, seepage areas of swamps; larvae carnivorous. Apparently characteristic of less stagnant and less acid situations than the larvae of *P. arguta*.

84. *Pilaria tenuipes* (Say).

Adult: crepuscular to diurnal; herbage and shrubbery of ravines and shaded rill or brook margins.

Immature stages: saturated silt, seepage areas, rill and brook margins; rarely taken in silt that borders non-flowing water; larvae carnivorous.

85. *Ulamorpha rogersella* Alexander.

Adult: crepuscular to diurnal; in Florida, known only from flood plain, hardwood swamps of western Florida; in North Carolina, taken from rhododendron and laurel thickets, bordering brooks at 4000 ft.

Immature stages: unknown. *U. pilosella* of northern states, lives in wet organic soil and is carnivorous.

86. *Eriocera fuliginosa* Osten Sacken.

Adults have never been taken in Florida; in Tennessee, the markedly crepuscular adults were confined to wooded creek and river margins.

Immature stages: in hard-packed, sand bottom of brooks and rills, beneath 2-6 inches of water; pupation (within breeding cages) in sand above water line; larvae carnivorous and voracious, feeding on large lumbriculid worms and other crane-fly larvae of nearly their own size.

87. *Penthoptera albitarsis* Osten Sacken.

Adult: crepuscular; herb and shrub strata, flood plain, low hammocks and hardwood swamps.

Immature stages: saturated and semi-suspended organic silt of seepage areas and rills within swamps; larvae carnivorous, active and voracious, feeding on other dipterous larvae and lumbriculid worms.

88. *Atarba picticornis* Osten Sacken.

Adult: largely nocturnal; herb and shrub strata, low and mesophytic hammocks and hardwood swamps.

Immature stages: sodden logs and branches in an advanced stage of wet decay; larvae ingest the wet, soft wood fibers; pupation within a silk-lined cocoon of wood fibers, near surface of rotten wood.

89. *Tricyphona inconstans* (Osten Sacken).

Adult: crepuscular; ferns and other rank herbage, open, or partially shaded, seepage areas and rill margins.

Immature stages: cool, saturated silt or sandy silt, seepage areas and rills; larvae carnivorous; pupation within silk lined vertical tubes whose mouths project slightly above the surface.

90. *Adelphomyia pleuralis* Dietz.

Adult: cool, damp, densely shaded bottoms of deep narrow ravines. All Florida records from ravines of Apalachicola River bluffs.

Immature stages: unknown. Closely related species occur in organic silt of cool, shaded, hillside seepage areas (Michigan and Indiana), and are carnivorous.

91. *Gnophomyia luctuosa* Osten Sacken.

Adult: crepuscular to diurnal; on trunks and exposed roots of the trees that contain the larval habitat (magnolia, beech, sweet gum, various oaks, red bay) usually in mesophytic woods or swamps. Oviposition into larval habitat, either through crevices in bark or on interior surfaces.

Immature stages: in reddish, sweet, waxy, rotten stuff produced by bacterial decay of heart wood of living trees; larvae feed on this rotten material.

92. *Gnophomyia tristissima* Osten Sacken.

Adult: crepuscular; herbs and shrub strata of mesophytic woods, usually on or near moist rotting logs.

Immature stages: moist, rotting hardwood logs and limbs, usually between loose bark and sap wood or in the inner bark; larvae feed on wet, pasty material produced by decay of wood.

93. *Teucholabis carolinensis* Alexander.

The only Florida specimens are some 40 adults taken from grasses and sedges of a fallow field in Manatee County, central Florida. The only other record is for the holotype, taken by Alexander in South Carolina, in 1916.

Immature stages: unknown.

94. *Teucholabis complexa* Osten Sacken.

Adult: crepuscular or nocturnal; herb and shrub strata of mesophytic hammocks, often on or in vicinity of logs, and brush piles. Oviposition into crevices and beneath edges of broken bark of hardwood logs.

Immature stages: rotten logs, between bark and wood or in wood. This is probably earliest crane-fly invader of rotting hardwoods in Florida and not often taken from logs in advanced stages of decay; large logs on well drained soil may be occupied for 2 or 3 years.

95. *Teucholabis lucida* Alexander.

Adult: crepuscular; rank herbage of deeply shaded ravines and sink holes; abundant year after year in a few isolated situations.

Immature stages: unknown.

96. *Gonomyia blanda* Osten Sacken.

Adult: crepuscular; herbage of open or partially shaded seepage areas and small, stream marshes.

Immature stages: saturated silt or silty clay, marshy situations.

97. *Gonomyia manca* Osten Sacken.

Adult: crepuscular or nocturnal; herb stratum of a wide variety of moist or wet situations.

Immature stages: wet to saturated sandy or semi-plastic earth.

98. *Gonomyia pleuralis* (Williston).

Adult: chiefly nocturnal or crepuscular; herbage, low hammocks, hardwood swamps, and swampy ravines.

Immature stages: saturated or semi-suspended black silt, margins of swampy pools, and fluctuating ponds in low hammocks; the larvae migrate with receding margins; larvae feed on algae and other living plant tissues.

99. *Gonomyia puer* Alexander.

Adult: crepuscular or nocturnal; herb stratum, cypress pond margins, and low, wet areas of flatwoods; less common along stream courses in hammocks.

Immature stages: wet sandy organic soils or sand-clay, stream margins and small local depressions in flatwoods.

100. *Gonomyia slossonae* Alexander.

Adult: apparently crepuscular; herbage of shaded seepage areas and rill margins.

Immature stages: saturated sand and sandy clay, small rill courses, rill margins and seepage areas; usually in basic soils produced by disintegration of limestones; larvae feed on living algae and on plant débris.

101. *Gonomyia subcinerea* Osten Sacken.

Adult: crepuscular; deeply shaded, moist situations, ravines, sinkholes and vicinity of hammock streams.

Immature stages: unknown.

102. *Gonomyia sulphurella* Osten Sacken.

Adult: crepuscular and diurnal; ground or low herbage of a wide variety of damp to wet situations.

Immature stages: saturated or barely submerged sand or sandy silt; larvae feed on algae and rootlets. Compact, saturated, bare or thinly grass-grown areas of nearly pure sand at the margins of brooks, marshes or lakes appear to be the preferred habitat.

103. *Ormosia brevicalcarata* Alexander.

The Florida records are from two deep, shaded, humid ravines in the Apalachicola River bluffs; the only other record is from the Great Smoky Mountains of North Carolina.

104. *Ormosia nigrapila* (Osten Sacken).

Adult: apparently crepuscular; herb stratum, low hammock and swamp seepage areas, and stream ravines.

Immature stages: saturated organic silt of cool, shaded seepage areas.

105. *Erioptera (Erioptera) osceola* Alexander.

Adult: crepuscular, frequently swarming at dusk; daytime habitat, herbage of well shaded rills, brooks and sandy seepage areas.

Immature stages: sandy silt and thin stratum of silt over sand, margins and bars, shaded rills and brooks; larvae herbivorous or scavenging.

106. *Erioptera (Erioptera) seminole* Alexander.

Adult: crepuscular to somewhat diurnal; rank ferns, lizard's tail, etc., margins of sphagnum growths, "bays" and bog streams.

Immature stages: saturated, strongly acid deposits of leaf débris and impure sphagnum, "bays" and bog streams; larvae herbivorous.

107. *Erioptera (Erioptera) septemtrionis* Osten Sacken.

Adult: crepuscular to nocturnal; cool, shaded ravines and wooded stream valleys.

Immature stages: wet to saturated organic soil, usually where there is definite flow of soil water.

108. *Erioptera (Erioptera) subchlorophylla* Alexander.

Adult: crepuscular to somewhat diurnal; luxuriant herbage of partially shaded, swamp streams and open swamp pools, hardwood and mixed swamps.

Immature stages: deep deposits of black ooze and semi-suspended silt, swamp streams and pools; larvae feed on algae and rootlets.

109. *Erioptera (Erioptera) vespertina* Osten Sacken.

Adult: crepuscular; herbage of muddy streams, marshes and sink-hole ponds, both shaded and unshaded situations; rare in swamps.

Immature stages: black, semi-suspended silt; sluggish stream and sink-hole-pond margins; frequently in margins of strongly polluted streams but not at all confined to pollution areas; larva ingests organic silt.

110. *Erioptera (Empeda) noctivagans* Alexander.

Adult: nocturnal; most records "At Light," flatwoods areas and vicinity of shrubby, flatwoods streams.

Immature stages: unknown.

111. *Erioptera (Mesocyphona) caloptera* Say.

Adult: largely crepuscular; ground and herb strata, wet, shaded situations.

Immature stages: saturated silt and wet organic mud, often in silt of small wet depressions, hardwood swamps, low hammocks, vicinity of streams and ponds.

112. *Erioptera (Mesocyphona) needhami* Alexander.

Adult: largely crepuscular; banks and herbage of seepage areas, rills and brooks.

Immature stages: saturated sand, sandy silt or sand-clay; basic to circumneutral seepage areas and rills.

113. *Erioptera (Mesocyphona) parva* Osten Sacken.

Adult: crepuscular and nocturnal; frequent in nearly all shaded or semi-shaded, permanently moist situations; ground and herb strata.

Immature stages: unknown.

114. *Erioptera (Mesocyphona)* sp., near *knabi* Alexander.

Adult: largely diurnal; scant herbage and wet sandy ground of unshaded flatwoods brooks and ditches; much more common in southern Florida.

Immature stages: unknown.

115. *Erioptera (Ilisia) graphica* Osten Sacken.

Adult: apparently crepuscular; herb and ground strata, densely shaded rills and seepage areas.

Immature stages: unknown.

116. *Erioptera (Ilisia) venusta* Osten Sacken.

Adult: crepuscular to diurnal; herbage of open or semi-shaded marshy streams, seepage areas and grass marshes. Oviposition into saturated pockets of silt.

Immature stages: saturated to very wet, organic soil and sandy silt.

117. *Molophilus floridensis* Alexander.

Adult: crepuscular to diurnal; mossy banks and herb and shrub strata, hammock brooks, seepage areas and ravines. Oviposition into steep or vertical, wet earth banks.

Immature stages: wet, rich soil or rill banks, often beneath moss.

118. *Molophilus forcipulus* Osten Sacken.

Adult: mainly crepuscular; herbage and low shrubbery of wide variety of shaded, wet situations.

Immature stages: wet, organic soil and saturated silt of stream margins.

119. *Molophilus pubipennis* (Osten Sacken).

Adult: apparently nocturnal; shaded, stream courses. Most Florida records are "At Light" and all for western Florida.

Immature stages: unknown.

120. *Molophilus* sp., *hirtipennis* group.

Adult: chiefly crepuscular; herbage of shaded rills and ravines.

Immature stages: saturated silt or silty loam, often beneath pieces of wood and bark; hammock and ravine rills and seepage areas.

121. *Dasymolophilus niphadias* (Alexander).

Adult: crepuscular; rank herbage of intrenched rills and brooks within deep shaded valleys and ravines. In the north (Michigan, Indiana, and Cumberland Plateau) a characteristic inhabitant of skunk-cabbage bogs.

122. *Helobia hybrida* (Meigen).

This common and widespread northern species is rare in Florida and largely confined to cleared seepage areas and roadsides of low flatwoods, where the adults occur within the sedge and grass stratum.

Immature stages (in the northern states): saturated organic soil of marshy situations.

123. *Trimicra anomala* Osten Sacken.

Adult: the few records are for sedge and rush zones of shallow lakes and marshes.

Immature stages: I have never found the immature stages but, in Europe, they have been taken from the muddy banks of a slowly flowing stream.

124. *Elephantomyia westwoodi* Osten Sacken.

Adult: crepuscular to somewhat diurnal; herb and shrub strata, moist hammocks and wooded stream valleys.

Immature stages: logs and limbs in an advanced stage of sodden decay; larvae ingest the soft wood fibers but probably feed mainly on mycelia of fungi.

125. *Toxorhina magna* (Osten Sacken).

Adult: crepuscular; ground, herb and shrub strata of hardwood swamps, especially the swamps of lake margins and the swampy margins (black-gum zone) of marshes.

Immature stages: unknown. A few larvae, provisionally identified as this species but never reared, have been taken from fragments of rotten wood imbedded in the saturated soil of swamps.

The two following species are reported from northern Florida by Johnson (1913): *Tipula cunctans* Say and *Nephrotoma pruinosa* (Johnson). The latter is known only from the holotype, described as *Pachyrhina pruinosa;* the former, I have never taken in Florida.

SUMMARY

1. Some 25,000 adult crane-flies and approximately 5,000 larvae and pupae were collected with detailed habitat notes from 22 counties of northern Florida during the years 1922 to 1931.
2. One hundred and twenty-five species are represented; of these approximately 70% are northern species that reach the southern limit of their ranges in Florida; the remainder are either Neotropical, or apparently endemic.
3. More or less complete breeding-cage life-histories of 74 of these species have been obtained and additional life-history and behavior data were secured by field and laboratory observations.
4. Nineteen of the typical features or complexes of topography, drainage, and vegetation, or "Major Habitats" of northern Florida are described.
5. The life cycle and other factors that affect habitat distribution of the crane-flies are described and discussed:

   a—Distribution of adults appears to be determined chiefly by the need for and reaction to low evaporation rates.

b—Specific habitats for the larvae are dependent upon the coincidence and maintenance of a number of factors including: food supply, moisture within rather narrow limits of toleration, and a medium that provides for the specific mode of respiration and locomotion.

c—Habitat distribution for the majority of the species is determined by the needs of the immature stages, chiefly the larval.

d—The extent of an individual major habitat is chiefly of importance as it affects a continuous supply of specific larval habitats and provides protection from prolonged drouths and ground fires.

6. The distribution of the species by major habitats, together with a summary of the general and Floridian geographic distribution of each species, is tabulated and a diagnosis of adult and immature stage habitats, as far as known, is given in the form of annotations to a species list.

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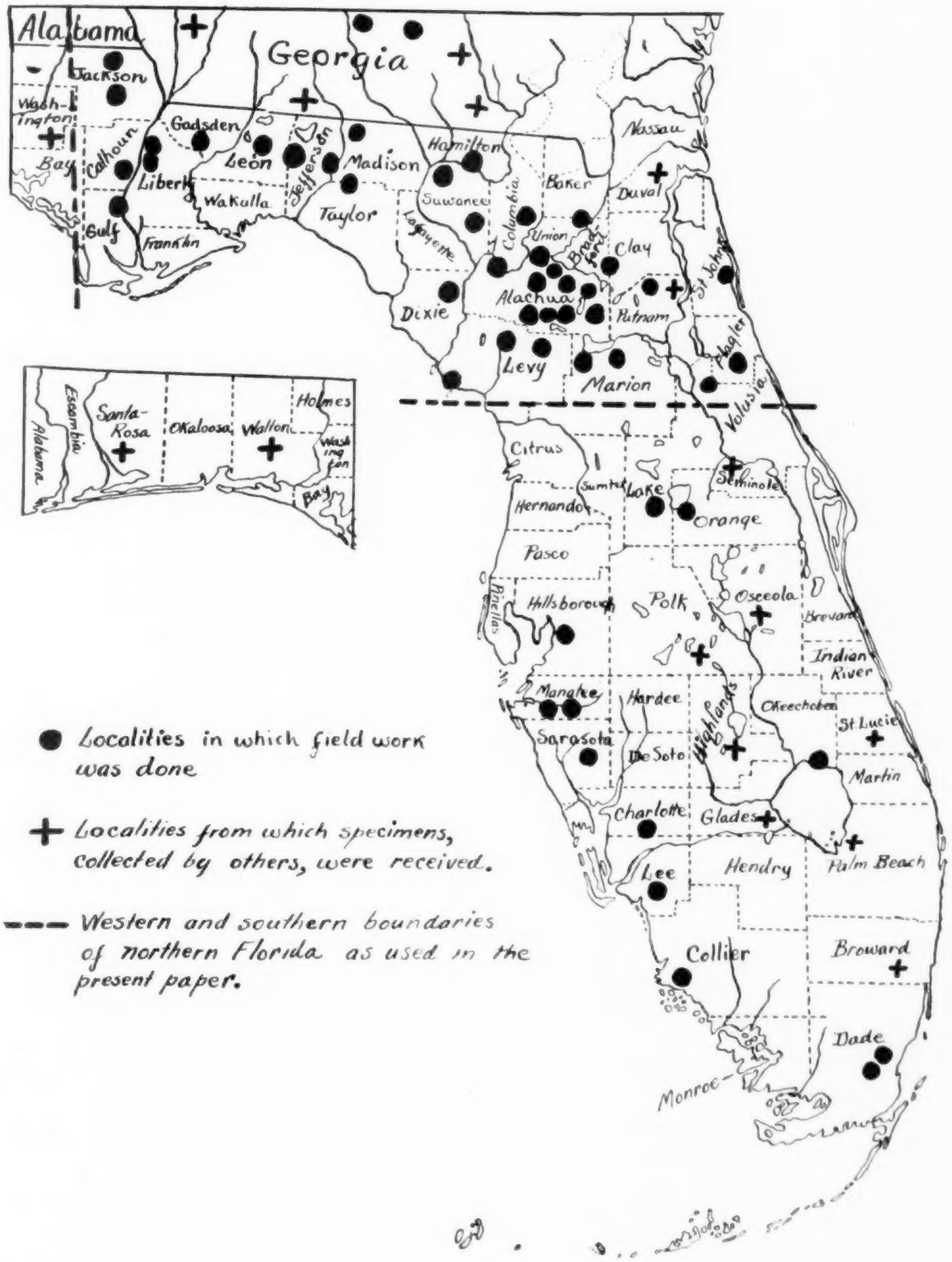

FIG. 1. County map of Florida showing areas in which field work was done.

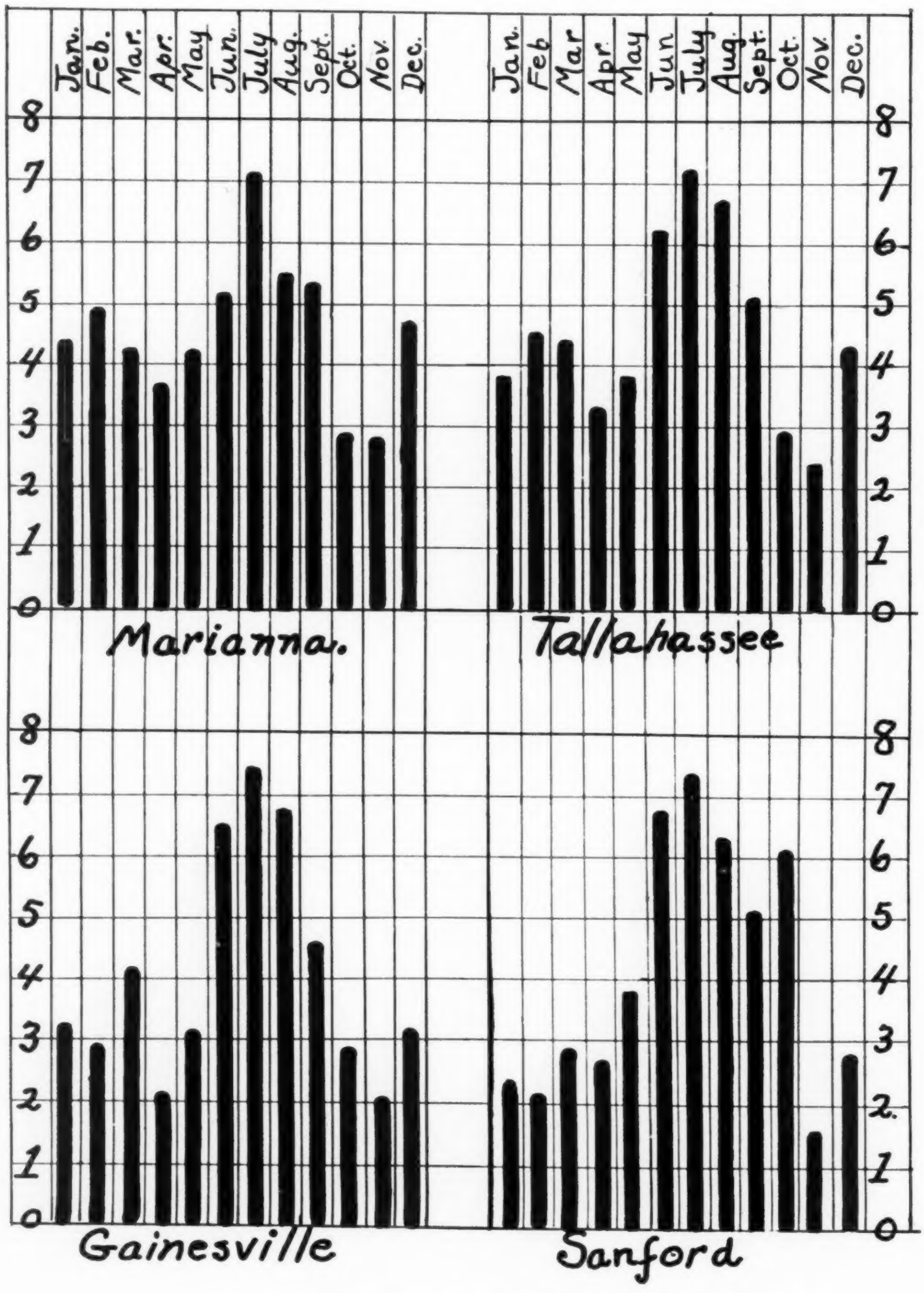

FIG. 2. Average monthly rainfall in inches, northern Florida.

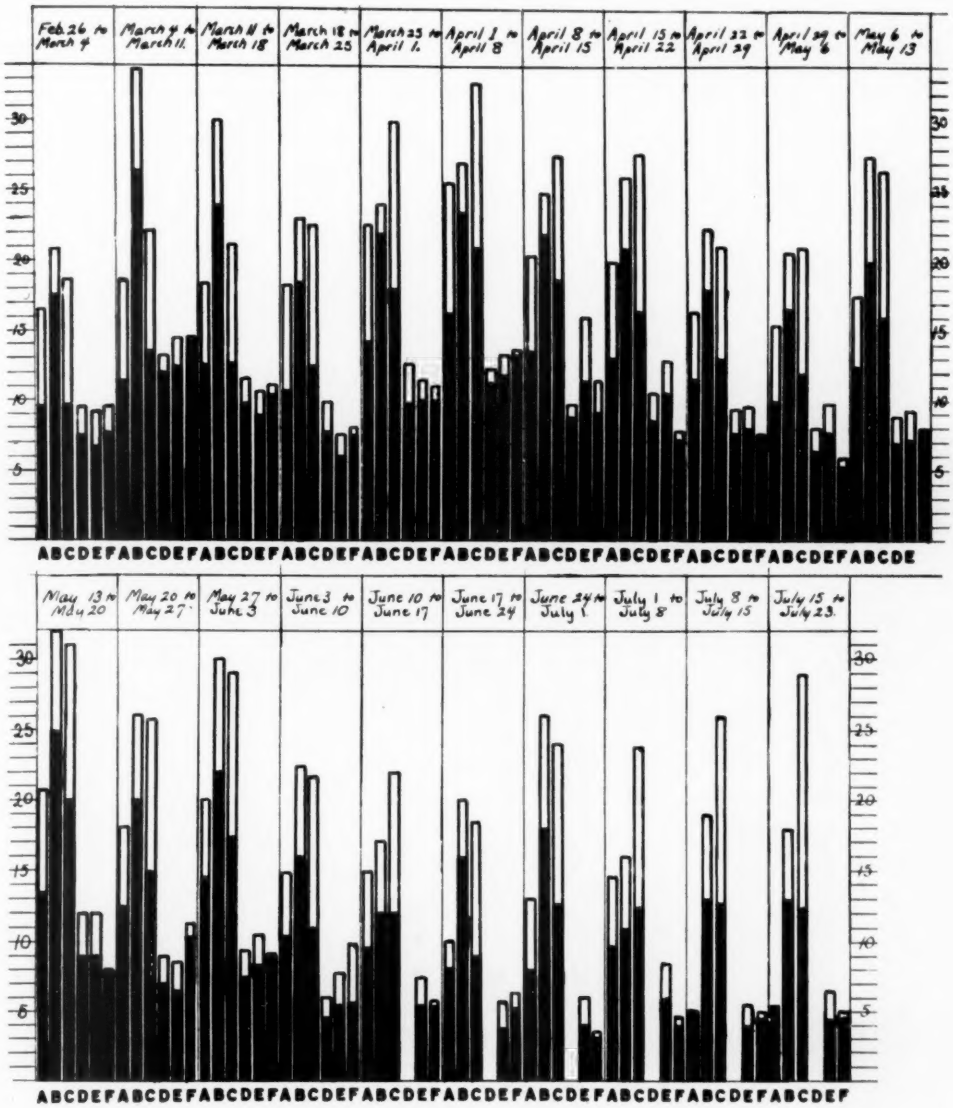

FIG. 3. Mean daily evaporation rates in milliliters for six types of contrasting major habitats in northern Florida.

Explanation of Figure 3. The black vertical column gives evaporation rate for a standard Livingstone white atmometer cup. The outlined extension of the black column gives the increment due to insolation as measured with a standard black cup. A—pine flatwoods. B—turkey-oak second growth. C—sand scrub. D—Hard wood swamp. E—mesophytic hammock. F—cypress swamp.

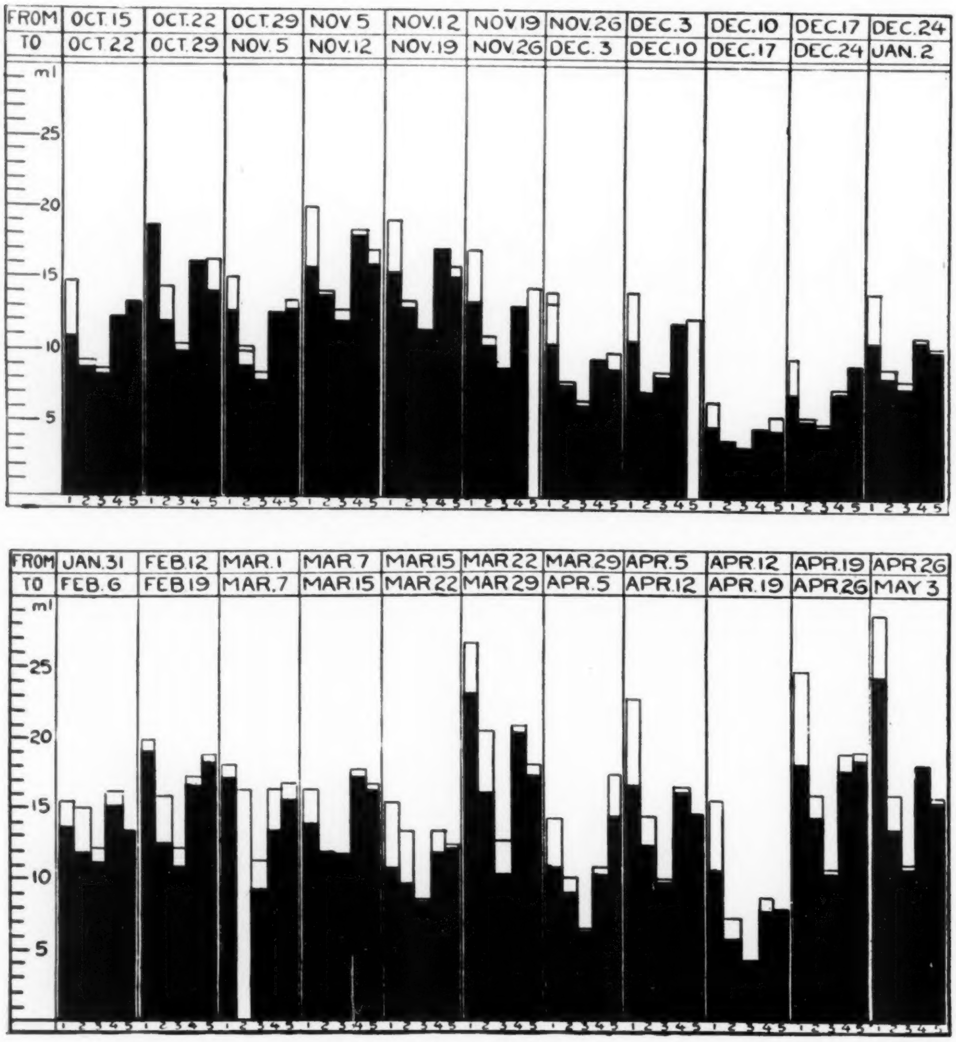

FIG. 4. Mean daily evaporation rate in milliliters for five stations in a wooded ravine and adjacent hardwood hammock, northern Florida (after Thone, 1927).

Explanation of Figure 4. The black columns and their outlined extensions have the same meaning as in Figure 3. 1—margin of cleared field, western margin of ravine. 2—wooded, middle slopes of ravine. 3—seepage area near bottom of ravine. 4—wooded eastern margin of ravine. 5—level hammock, 20 yards east of ravine.

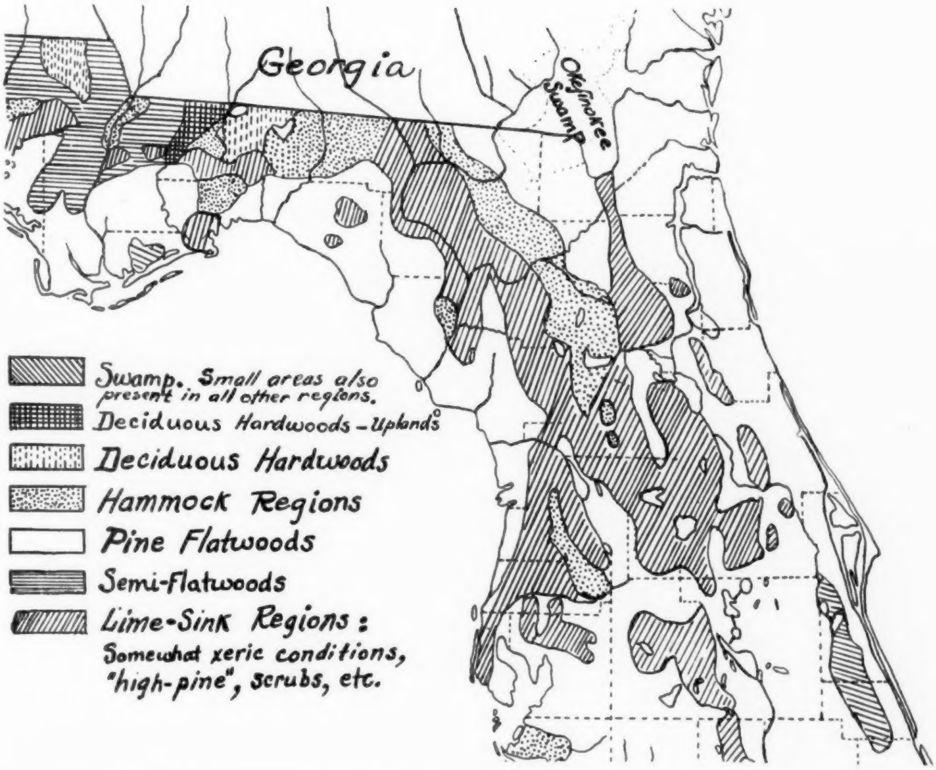

FIG. 5. Phytogeographic map of northern and central Florida, after Harper.

FIG. 6. Hog-Town Creek, Alachua County, October 15, 1923.
FIG. 7. Rattle-Snake Branch, Alachua County, October 13, 1923.
FIG. 8. Spring rill, mesophytic hammock, Alachua County, June 2, 1928.
FIG. 9. Shaded sink-hole pond, Alachua County, May, 1928.

FIG. 10. Biven's Arm of Payne's Prairie, Alachua County, March 3, 1927.
FIG. 11. Biven's Arm of Payne's Prairie, April, 1928.
FIG. 12. Larger calcareous stream, Sante Fe River, April 28, 1927.

FIG. 13. Flatwoods and cypress pond margin, Bradford County, November, 1929.
FIG. 14. Swamp stream, hardwood swamp, Alachua County, May, 1928.
FIG. 15. Flood plain swamp, Sweetwater Creek, Liberty County, April 25, 1924.

FIG. 16. High hammock, Marion County, April 16, 1930.
FIG. 17. Mesophytic hammock, Alachua County, May 4, 1929.
FIG. 18. Bottom of Torreya Ravine, Liberty County, April 24, 1924.
FIG. 19. Bottom and lower south slopes of Devil's Mill Hopper, Alachua County, June 2, 1928.

Fig. 20. Black gum zone, Sugar Foot Prairie, Alachua County, March 15, 1923.
Fig. 21. Seepage area, upper slopes of Devil's Mill Hopper, June 2, 1928.
Fig. 22. Turkey oak, second growth, high-pine land, Alachua County, April, 1929. The white spots are "salamander" mounds.
Fig. 23. Interior of cypress swamp, drouth conditions.
Fig. 24. Black gum swamp, lower Hog-Town Creek, October, 1923.
Fig. 25. Marshy rill course, Liberty County, April, 1924.

THE VEGETATION OF THE PIKE'S PEAK REGION

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THE VEGETATION OF THE PIKE'S PEAK REGION

I. INTRODUCTION

The Pike's Peak Region

The Pike's Peak region lies in the east-central part of Colorado, about 38°30″ north latitude and 106° west longitude. The mountain itself is approximately eighty miles by airline from the Great Continental Divide. It rises abruptly from the Great Plains to its high altitude in a little more than seven miles by airline. These facts give the region characteristics peculiar to itself, and have affected vegetational development.

The Pike's Peak region has long been outstanding as a center for scientific investigations. The chief reason for this is the wide range of climate and vegetation from base to summit. A second reason is the easy accessibility of the mountain. The summit, which is 14,109 feet above sea level, can be reached by train via the Cog Railway, by auto over the Auto Highway, as well as by foot over well-marked trails (Fig. 1). Moreover, the Pike's Peak

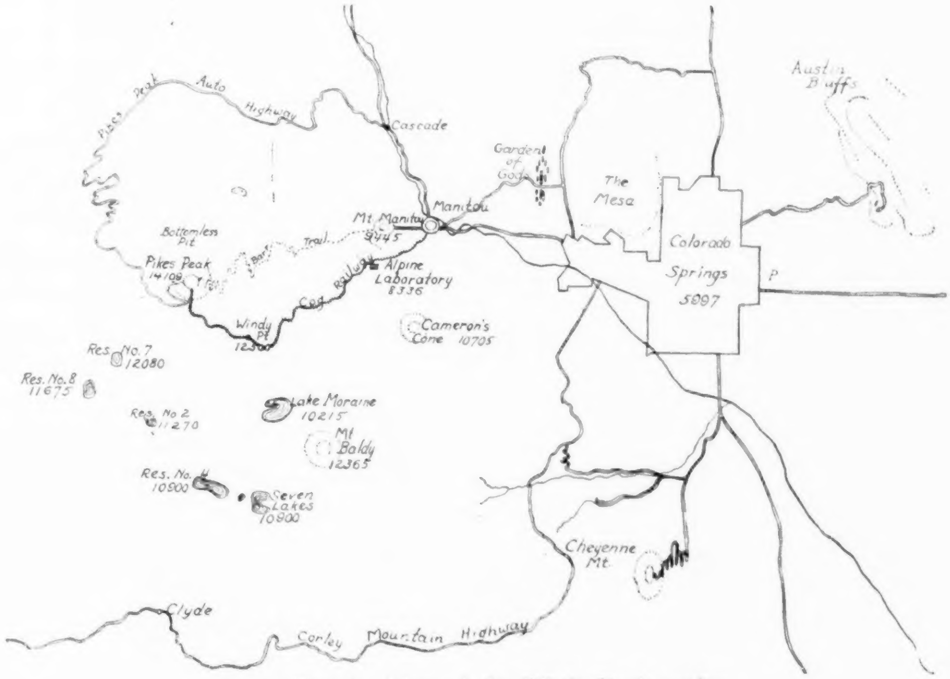


FIG. 1. Map of the Pike's Peak region.

region affords exceptional opportunities for ecological study because it has long been a center for research. The Alpine Laboratory was established in 1900 and has served as a base for Ecological Research by the Carnegie Institution of Washington since 1918, while the Fremont Experiment Station of

the Forest Service was established in 1910. The materials for this paper are drawn from the present projects in adaptation and climax at the Alpine Laboratory, and for the use of these the writer wishes to express his obligation to the Carnegie Institution.

Comparison With Other Rocky Mountain Regions of Colorado

The Pike's Peak region belongs properly to the Southern Rockies, which, according to Rydberg (1916), extends from the Santa Fe Mountains in New Mexico to the Medicine Bow Mountains in southern Wyoming. This area differs, however, from other regions in this range in several respects.

In the first place, since the region is on the eastern slope of the range and extends far out into the Great Plains, it is not uncommon to find many of the plants abundant in eastern Colorado and states farther east wandering far up in the mountains. Some species, as is the case of *Artemisia frigida*, are present at altitudes to approximately 10,000 feet. Others, such as *Andropogon scoparius*, and species of Bouteloua, Astragalus, and Opuntia, are present well over 8,000 feet.

In the second place, several dominant species abundant in other regions drop out in this area. *Pinus murrayana*, abundant to the west and found farther north, and *Abies lasiocarpa*, present all the way from New Mexico and Arizona to Alaska, are practically unknown here. The former is the most common conifer of the montane zone of the Northern Rockies, and is present only in the northern part of the Southern Rockies. Two or three individual specimens have been reported in the neighborhood of Pike's Peak, but the pine is most abundant in the vicinity of James, Evans, and Long's Peaks. As far as is known, *Abies lasiocarpa* is entirely absent. Moreover, a number of alpines common on the Continental Divide are rare or absent on Pike's Peak.

In the third place, the annual rainfall is higher in the Pike's Peak region than in areas of approximately similar altitudes on the eastern slope (Table I). Examination shows that the precipitation is from 7 to 24 per cent higher at the Pike's Peak stations. In spite of the higher rainfall, drier conditions prevail in this area because of its southward projection into the Great Plains at a considerable distance from the Continental Divide. This feature of the climate probably accounts in part for the scarcity of individuals as well as species, when compared with other mountainous regions to the north and west.

II. VEGETATION

The vegetation of the Pike's Peak region, like that of other mountainous areas, falls naturally into altitudinal zones (Figs. 2, 3). The emphasis in this treatment of the vegetation is placed on the abundance and distribution of

TABLE I. *Average annual rainfall at various stations in Colorado, 1910-1930. (Climatological data, Weather Bureau, U. S. Dept. Agr.)*

Station	County	Elevation	Inches of Rainfall	Difference	
				Inches	Percent
Pike's Peak Fremont Exp. Station	El Paso	8,836	22.01		
Auldhurst	Teller	8,500	16.97	—5.04	—23.9
Dillon	Summit	8,800	17.42	—4.59	—20.9
Estes Park Fish Hatchery	Larimer	8,000	19.62	—2.39	—10.9
Fraser	Grand	8,671	20.33	—1.68	— 7.63
Pike's Peak Subalpine Lake Moraine	El Paso	10,265	24.62		
Leadville	Lake	10,248	19.82	—4.80	—19.7
Victor	Teller	10,100	18.72	—5.90	—24.0

those species which dominate at the present time, and the more important subdominants. Extensive lists of species of the various climaxes or zones can be secured from Clements' writings (1916, 1920). All plant names given in this paper were taken from Clements and Clements "Rocky Mountain Flowers" (1928).

PLAINS

The Pike's Peak region is bordered on the east by that part of the grassland known as the Great Plains. This is a vast region of level plains and gently rolling prairie, dissected by streams and covered with grasses. The most characteristic genera of the Great Plains at present are Bouteloua, Bulbilis, and Aristida. Stipa, Agropyrum, Sporobolus, and Andropogon may be found along railroad cuts, gullies, and draws. Scattered over the Great Plains are cacti, yucca, legumes, composites, and many small, xerophytic, flowering herbs (Fig. 4).

Shantz (1905) in a most interesting paper deals with the vegetation of the mesa region east of Pike's Peak. He correlates the vegetation of the area with the topography, climate, and types of soil. At the base of Pike's Peak the mixed prairie aspect of the Great Plains becomes evident. The dominants of the association which occur here are *Stipa comata, Agropyrum glaucum, Sporobolus cryptandrus, Koeleria cristata, Bouteloua gracilis,* and *Bulbilis dactyloides.* The midgrasses, Stipa, Agropyrum, Sporobolus, and Koeleria, are shorter than their eastern relatives because of the lower rainfall and intense grazing.

Disturbances of varied nature have checked the widespread development of the midgrasses. As a result, *Bouteloua gracilis* is the most conspicuous of all the grasses from the standpoint of abundance and distribution. It is the abundant climax species found in all the areas examined. *Stipa comata* occurs on elevated ridges and roadsides, *Agropyrum glaucum* on moist areas, like ditch or stream banks, *Sporobolus cryptandrus* in long-abandoned fields.

FIG. 2. Transect through different climates from plains grassland near Colorado Springs to alpine tundra, Pike's Peak.

and especially in sandy soil, and *Koeleria cristata* in more favored places of higher water content, such as north slopes. Other grasses of lesser abundance are: *Bouteloua hirsuta,* favoring more xerophytic habitats than does *Bouteloua gracilis; Bouteloua racemosa,* confined to more mesophytic habitats than is *Bouteloua gracilis; Muhlenbergia gracillima,* ranking next to *Bouteloua gracilis* in abundance and occurring in overgrazed areas and xerophytic habitats; *Stipa viridula,* abundant in xerophytic and over-grazed areas; *Calamovilfa longifolia* and *Aristida sp.,* growing on sandy soils and dry lime ridges; and *Andropogon scoparius,* occurring on alluvium, cut-back gullies, and sandy ridges.

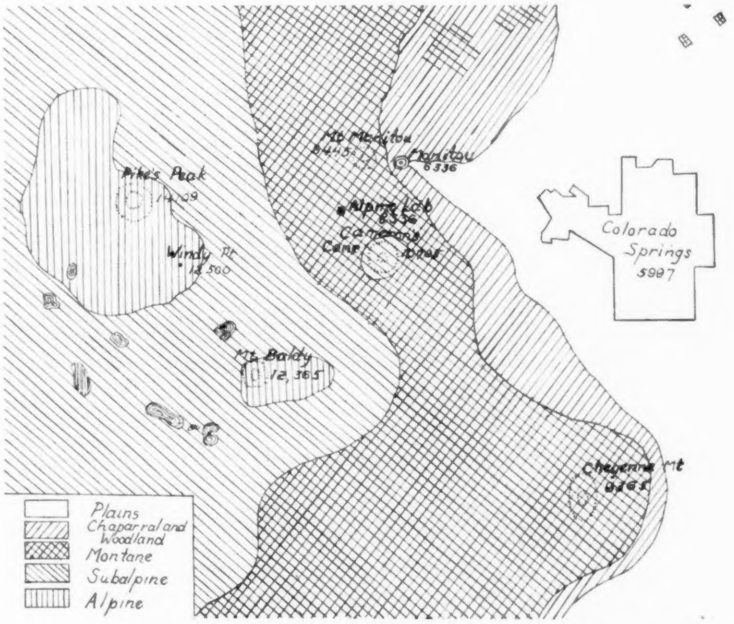


FIG. 3. Rough vegetation map of the Pike's Peak region.

Conspicuous seasonal aspects are evident. In early spring, societies of *Pulsatilla hirsutissima, Townsendia exscapa,* and *Leucocrinum montanum* are to be found in dry habitats on northern exposures. Later *Senecio aureus, Yucca glauca,* and *Astragalus drummondi* alternate in importance over practically the entire area. Any one of the species, but *Yucca glauca* more commonly than the others, may assume a subdominant aspect. Other important vernal species occurring widely and often forming societies are *Thelesperma gracile, Pentstemon secundiflorus, P. unilateralis, P. angustifolius, Euphorbia robusta, Arenaria fendleri, Opuntia polyacantha, Lesquerella montana, Aragalus lambertii, Gaura coccinea, Astragalus crassicarpus,* and various species of *Erigeron.* During the summer the societies become more conspicuous, the most important being constituted by typical mixed prairie species, such as *Artemisia frigida, Gutierrezia sarothrae, Chrysopsis villosa, Lupinus argen-*

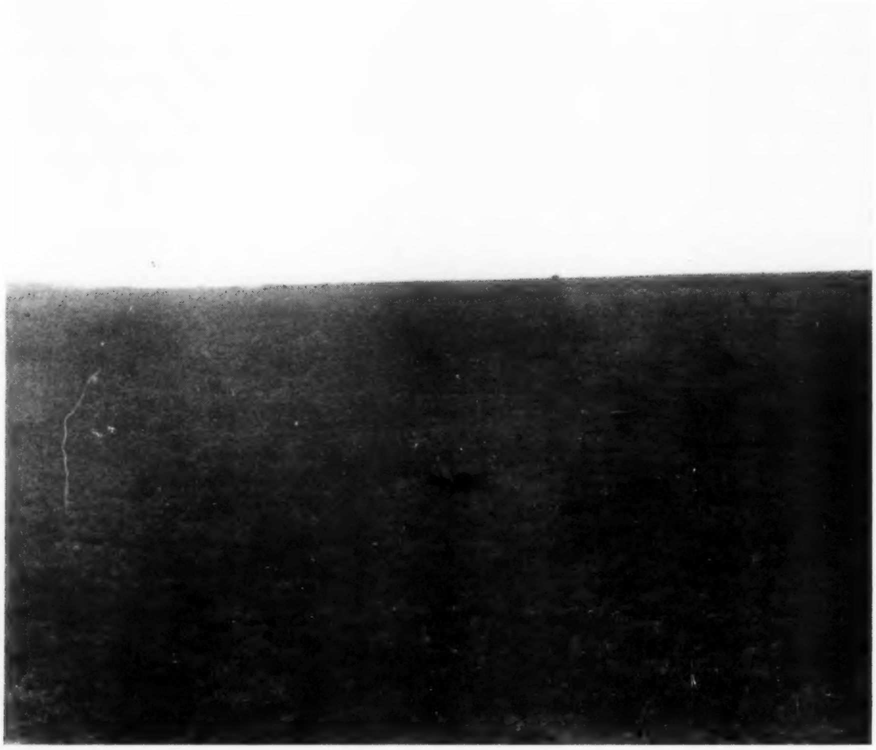


FIG. 4. Great Plains: Bouteloua, Bulbilis, Opuntia, Carduus.

FIG. 5. Oak-chaparral, midground; Western yellow pine on ridge; grasses in foreground.

teus, Plantago purshi, Lepachys columnaris, and *Argemone platyceras.* The autumnal or serotinal aspect is characterized by *Senecio douglasi, Grindelia squarrosa, Carduus undulatus, Liatris punctata, Artemisia campestris, A. ludoviciana, Gymnolomia multiflora,* and certain species which have continued from the preceding period.

CHAPARRAL AND WOODLAND

The chaparral and woodland formations are poorly represented in the Pike's Peak region. The species of these zones do not dominate over large areas as those of the other zones do. The dominants of these two climaxes are limited to a very small area between the plains and montane regions, since the plains sometimes rise as high as 7,000 feet, and the montane often pushes down to 6,350 feet. At various points in the region the plains and montane zones come together, forming savannah, thus eliminating the chaparral and woodland formations entirely; at other places there is a mixture of some of the dominants of all four of the zones; and at others either chaparral or foothills species, or both, may form a slight tension zone between the plains and montane species. This lack of definite order is conspicuous, and the chaparral and woodland climaxes are treated together because they are found in such limited areas, are represented as relicts in this region, and because the dominants of the two formations are found intermixed.

There is evidence to indicate that the chaparral is advancing, but the natural limits of this formation are hard to define. In most areas intense grazing has destroyed the chaparral, permitting the prairie to advance. The best expression of this formation is to be found on southern exposures of ravines and canyons of the montane zone, in areas where its dominants mix with the *Pinon-Juniper* woodland, as on small plateaus like the Garden of the Gods, and the foothills proper like those back of Manitou. The conspicuous dominants of the chaparral are *Quercus gambeli, Q. gunnisoni, Rhus trilobata, Cercocarpus parvifolius, Holodiscus dumosa, Rubus deliciosus, Prunus demissa, Symphoricarpus occidentalis,* and *Ribes cereum.* The woodland dominants of the foothills are *Pinus edulis* and *Juniperus monosperma scopulorum.* The oaks are the most important of the climax species. They are abundant on the hills and slopes above the grassland, in areas where grasses and western yellow pine meet, and in ravines and canyons up to 8,500 feet (Fig. 5). Most of the other dominants are restricted to certain habitats and are more sparse. *Cercocarpus parvifolius* is next in abundance and closely associated with the oaks. It is more widespread, occurring on scattered bluffs and ridges, in the tension zones, and as an invader in the grasslands. It is present well over 9,000 feet on south slopes and ridges. *Rhus trilobata* is closely associated with Cercocarpus in the lower foothills, and occurs with Pinus and Juniperus more commonly than any of the other species except *Cercocarpus parvifolius.*

The *Pinus-Juniperus* formation is best expressed in areas like the foothills around Manitou, but relics have been found as high as 8,500 feet. Ribes and Symphoricarpus are frequent in the lower foothills and are found sparingly associated with Holodiscus, Prunus, and Rubus up to altitudes of 9,000 feet.

MONTANE ZONE

The montane formation is the most extensive of the six zones represented in the Pike's Peak region. It is here considered to lie between the altitudes of 6,500 and 9,000 feet, although some of its dominants extend downward through ravines, canyons, and on north slopes to an elevation of 6,350 feet, and upward on warm slopes to 10,000 feet. The climax species are *Pseudotsuga mucronata, Pinus ponderosa, P. flexilis, Abies concolor,* and *Picea pungens.*

Since, as evidences indicate, there has been less disturbance in the montane formation than in any other part of the region, practically all the dominants attain large size and are widely distributed. *Pseudotsuga mucronata* and *Pinus ponderosa* are the two most important species. The former is found chiefly on north slopes, where it forms dense forests, and sparingly on the south slopes, where it mixes with western yellow pine (Fig. 6). Almost pure stands of the Douglas Fir are found between elevations of 6,500 and 8,000 feet. Above 8,000 feet it mixes more frequently with *Picea pungens, Pinus flexilus, Abies concolor* and *Pinus ponderosa.* In favored spots in these higher altitudes, as in Hurricane Canyon, specimens of Douglas Fir two feet in diameter are to be found. Pseudotsuga reproduces abundantly and it is rare to find the ruderal dominants, aspen and limber pine, flourishing over very large areas in the Douglas Fir territory. It is found sparingly above 9,000 feet, and disappears between 9,500 and 10,000 feet.

Closely associated with *Pseudotsuga* is *Pinus ponderosa.* This species occurs on the more open slopes and ridges over large areas between 6,500 and 10,000 feet. Relics of a western yellow pine forest that once covered the entire region are found on scattered bluffs and ridges outside of Colorado Springs. Because of its intolerance the western yellow pine does not grow in dense stands, as does the Douglas Fir. The Black Forest is the best expression of *Pinus ponderosa* in the Pike's Peak region. The forest is eighteen miles northeast of Colorado Springs, 7,000 feet in elevation, and approximately thirty-one miles long and twenty miles wide. Being higher, the forest receives a greater rainfall than the surrounding region, and is consequently able to maintain itself. Although it cannot be stated definitely, conditions seem to indicate that the forest is advancing into the grassland. Aside from a scattering of climax Douglas fir, the Black Forest is a savannah-like growth of western yellow pine, *Bouteloua gracilis, B. racemosa, Stipa comata, S. scribneri, Agropyrum glaucum, Sporobolus cryptandrus,* and *Andropogon*

FIG. 6. Montane: *Pseudostuga-Pinus* climax.

scoparius. Montane and plains subdominants, such as Arctostaphylus, Besseya, species of Solidago, Erigeron, etc., mix here. *Pinus ponderosa* is also found in the upper chaparral and foothills mixing with the dominants of these two climaxes. Above 7,000 feet it is limited to the south slopes, ridges, and parks. The largest specimens of western yellow pine are to be found between 8,000 and 9,000 feet; above this altitude the individuals are smaller. The upper limit of western yellow pine is slightly over 10,000 feet.

The remaining dominants, *Abies concolor, Pinus flexilis,* and *Picea pungens* do not occur in sufficient abundance in any area to become of climax importance. *Abies concolor*, present throughout the zone, is confined mainly to the canyons, ravines, and other protected spots, although a limited amount is found mixing with Douglas fir on north slopes. Its largest specimens are found in canyons, North Cheyenne Canyon for example, at altitudes of approximately 7,500 feet. *Pinus flexilis* is found both mixing with the Douglas fir and western yellow pine, and forming an ecotone between those two species. *Picea pungens* is limited almost wholly to the canyons and ravines.

The montane region is rich in subdominants, the most conspicuous of which are *Populus tremuloides, Rosa acicularis, Rubus deliciosis, Chamaenerium angustifolium,* and species of Geranium, Erigeron, and Solidago.

Subalpine Zone

In the Pike's Peak region, the subalpine zone is considered to lie between the altitudes of 9,000 feet and 11,500 feet or timberline. The characteristic subalpine trees are *Picea engelmanni*, *Pinus aristata*, and *P. flexilis.*

In the lower part of the subalpine zone *Picea engelmanni* is present in canyons and ravines and scattered through the more abundant *Populus tremuloides.* On the high mountain slopes near timberline, Engelmann spruce, or white spruce, forms dense thickets. In these localities *Populus tremuloides* is scarce or absent. *Pinus aristata* is a close associate of the Engelmann spruce. All three of the dominants and *Populus tremuloides* are present at timberline. Here, however, the latter dwarfs down to a height of one or two feet, and occurs only occasionally, as do *Pinus flexilis* and *Juniperous sibirica. Pinus flexilis* occurs throughout the zone, the tallest trees of the species being located at approximately 11,000 feet. Engelmann spruce and foxtail pine are the important timberline species. The former is perhaps the more abundant of the two, and has been found in the protection of rocks as high as 12,200 feet. It is not uncommon to find clumps of dwarfed Engelmann spruce and foxtail pine growing a little above timberline in the alpine meadow. *Pinus aristata,* which mixes equally with the other two dominants, is more abundant toward timberline, the largest specimens of this species occurring also at approximately 11,000 feet. Approaching timberline, all the trees become smaller and in most places assume the krummholz habit. At timberline Engelmann spruce is stunted, with the lower branches elongated and growing close to the ground; foxtail pine is gnarled and twisted, with the branches short and few on the windward side.

The subalpine undergrowth is characterized not only by many of the same species found in the montane and alpine climaxes, but also different species of the same genera. Some of the more conspicuous shrubs and herbs are *Dasyphora fruticosa, Sambucus racemosa, Salix planifolia, S. chlorophylla, S. monticola, Betula glandulosa, Saxifraga jamesi, Pedicularis procera, P. canadensis, Pentstemon glaucus, Primula parryi, Rhodiola rosea, Erigeron subtrinervis, Solidago multiradiata, Valeriana silvatica, Senecio bigelovi, Caltha rotundifolia, Mertensia sibirica, Rydbergia grandiflora,* and *Gentiana frigida. Salix brachycarpa, S. pseudo-lapponum,* and *Dasyphora fruticosa* often form an ecotone between the alpine meadow and the subalpine forest.

The subalpine climax is further characterized by "parks," the principal species of which are *Populus tremuloides, Pinus ponderosa,* and species of Danthonia, Festuca, Poa, and Agropyrum.

Alpine Tundra

The alpine zone extends from timberline to the summit of Pike's Peak, 14,109 feet. Timberline, the lower limit of the alpine tundra, varies with a

number of factors, chiefly exposure. Its approximate altitude in the Pike's Peak Region is 11,500 feet, although the tree line is commonly higher on north slopes, in ravines, and other protected areas.

The alpine region is conveniently divided into two divisions, the low alpine and the high alpine. The low alpine contains comparatively few rocks and boulders and lies approximately between timberline and 13,000 feet. It is the transition region between subalpine and alpine. In this area are to be found the woody plants of the alpine zone, as well as certain herbaceous species which have invaded from the lower zones and maintained a foothold here. A further distinction of the low alpine is the fact that most of the alpine meadows, in which are scattered numerous gopher mounds, are found here (Fig. 7).

FIG. 7. Alpine tundra: *Elyna* climax.

The conspicuous dominant of the low alpine is *Elyna bellardi*, while *Artemisia scopulorum* and *Carex rupestris* are the important subdominants. Elyna, in the meadows proper, and Artemisia, in protected places, cover large areas between timberline and 12,500 feet. *Carex rupestris* is here found to a limited extent in disturbed places and more rarely mixed with Elyna. Carex reaches its greatest abundance between 12,500 and 13,000 feet. Elyna is almost entirely absent in this higher area. It is apparently limited, as a

climax species, to the lower altitude in the Pike's Peak Region as well as on James, Evans, and probably other northern peaks.

The woody plants of the alpine region are limited to three, *Dryas octopetala* and *Salix saximontana*, which are more abundant on north slopes but are also found in protected places on south slopes, and *Dasyphora fruticosa*, found throughout the alpine tundra on both north and south exposures.

The alpine tundra has a large number of conspicuous subdominants, some of which are *Androsace chamaejasme*, *Polemonium confertum*, *Castilleia pallida occidentalis*, *Polygonum viviparum*, *Mertensia alpina*, *Luzula spicatum*, *Rydbergia grandiflora*, and *Festuca brachyphylla*.

The gopher mounds, caused by a species of pocket gopher, *Thomomys fossor*, vary in structure from the typical alpine tundra in which they are located. Soon after a spot has been denuded by the pocket gopher either *Sieversia turbinata*, *Polemonium confertum*, *Polygonum bistorta*, or *Mertensia alpina* may invade the area and hold it for a long period to the possible exclusion of other species. Usually, however, a number of species, such as those of Sieversia, Polemonium, Polygonum, Mertensia, and *Agropyrum scribneri* enter the mound. These species can well be called ecological equivalents, since it is most unusual to find one giving way to another because of non-living environmental factors. *Dasyphora fruticosa*, shrubby cinquefoil, eventually becomes the outstanding dominant of the majority of mounds, although in a few of them, especially at higher elevations, this species is not found. The shrubby cinquefoil enters from the meadows where it grows sparingly and is of small size. It may enter the mounds immediately or at various intervals, depending on the abundance of other species present. Here it becomes two or three times larger than it is in the meadows. All species show a better growth in the gopher mounds.

The high alpine, extending from 13,000 feet to and including the summit, lies above the majority of the meadows. It is a large boulder field with few or no gopher mounds, and its vegetation is confined to little patches among the rocks where water seeps out. These wetter areas are dominated almost exclusively by *Mertensia alpina*, *Caltha leptosepala*, and species of Carex and Poa. In the drier places, among the rocks, *Senecio fremonti* is abundant, and the yellow form of *Castelleia p. occidentalis* is replaced by the red-colored variety. The main species of flowering plants which range throughout the high alpine to the summit are *Gentiana frigida*, *Saxifraga nivalis*, *Poa alpina*, *Festuca brachyphylla*, *Oreobroma pygmaea*, *Claytonia megarrhiza*, *Elyna bellardi*, and *Oxyria digyna*.

A number of lichens are found throughout the Pike's Peak Region, but only in the high alpine zone do they approach dominance. Some of the more conspicuous species found above timberline are *Gyrophora rugifera*, *Caloplaca elegans*, *C. elegans v. muscicola*, *Cetraria juniperina*, *Rhizocarpon geograph-*

icum, *Parmelia conspersa*, *P. conspersa v. hypoclista*, and *Cladonia* sp. A lichenous crust, consisting of a Cladonia and possibly *Lecidea granulosa*, is found in snow pockets. Most of the lichens are encrusting, except Gyrophora, which belongs to the foliose group. The foliose, crustose, and fruticose groups are about evenly distributed throughout the climatic zones of the entire region. Parmelia, Peltigera, and Cladonia are the most widespread genera, while *Usnea barbata*, *Cladonia pyxidata*, and *Caloplaca elegans* are the most abundant species.

III. PHYSICAL FACTORS

One instrumental station was located on the south slope at Windy Point, at an altitude of 12,150 feet; another on a level area between the north and south exposures at the laboratory, 8,336 feet; and a third on the plains (Fig. 1) east of Colorado Springs, 5,990 feet. At various times substations were established in the lower subalpine, 9,300 feet, at the base of a south slope; in the subalpine, 11,000 feet, in the climax forest; and on Pike's Peak, 14,109 feet, among the rocks a little below the summit. The data secured from these substations have been incorporated with that of the main stations.

AIR PRESSURE

There is a decrease of air pressure with increased altitude (Table II).

TABLE II. AIR PRESSURE AT DIFFERENT ALTITUDES

Altitude (feet)	*Air pressure (inches)*
0.0	30.000
1640.43	28.307
3280.8	26.693
4921.2	25.157
6561.7	23.622
8202.1	22.283
9842.5	20.905
11482.9	19.724
13123.3	18.504
16404.2	16.339

Altitude is only a remote factor in plant growth however. The varying climatic conditions at the different elevations are the direct factors to be taken into account.

TEMPERATURE

As a rule in Colorado, an increase in elevation of 1,000 feet decreases the mean temperature for the year about 2½°, spring 3½°, summer 3°, fall 2½°, and winter 1½°. There is also a decrease in the difference between the mean temperature of the warmest month and that of the coldest month, and a greater difference between sun and shade and day and night temperatures.

Daily air temperature decreases with increased altitude (Fig. 8). A difference of 8° F. in air temperature exists between the plains station and the montane station. A somewhat greater difference, 17° F., is found between the

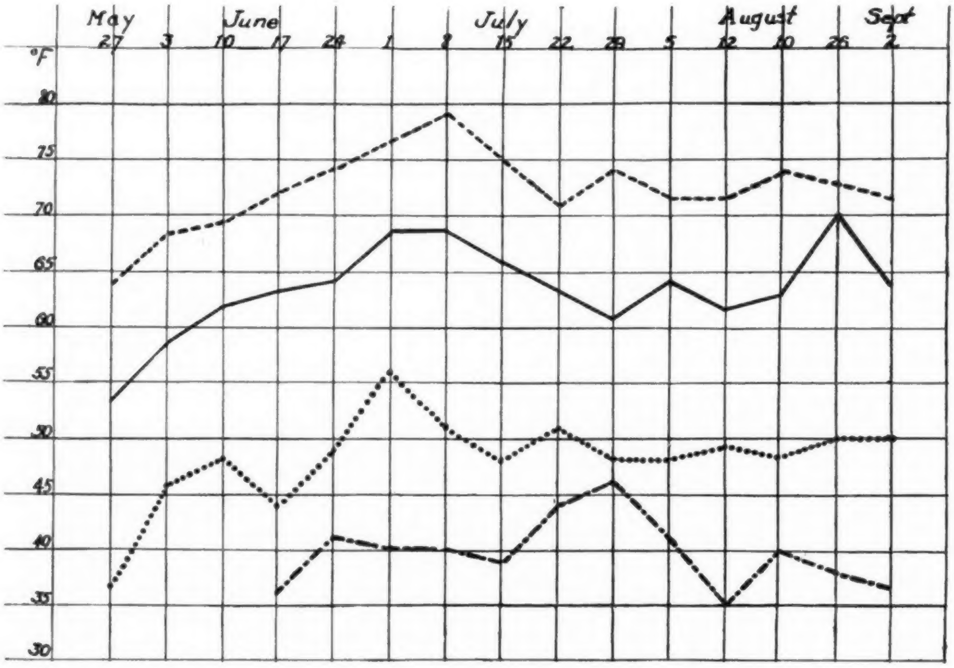


Fig. 8. Average day air temperature, by weeks, 1927-30; Peak, 1928. Legend: Plains— — — —; Montane————; Alpine . . . .; Summit of Peak — - — - —.

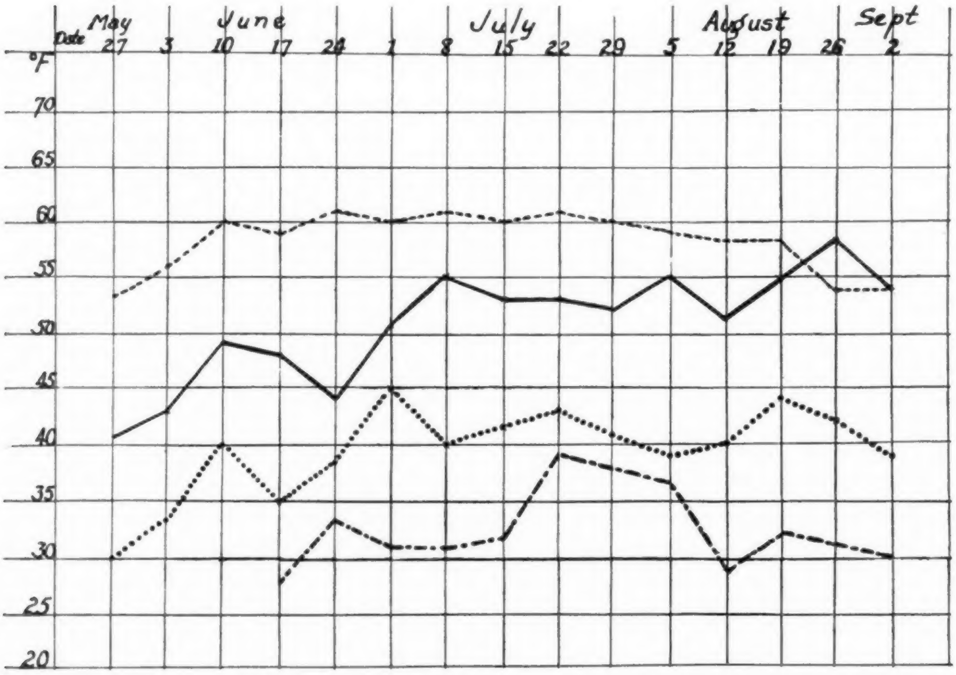


Fig. 9. Average night air temperature, by weeks, 1927-30; Peak, 1928. Legend: Plains— — — —; Montane————; Alpine . . . .; Summit of Peak — - — - —.

montane and alpine stations, and a 7° difference between the alpine and peak stations. The day temperature averages for the whole period were 72, 64, 47, and 40° F. for the plains, montane, alpine, and peak stations respectively. The average night air temperatures for the four stations were 58, 50, 39, and 33° F., showing differences of 8° between the plains and montane stations, 11° between the montane and alpine, and 6° between the alpine and summit (Fig. 9). These results are in accord with those secured during earlier studies from 1900 to 1909 and from 1918 to 1923.

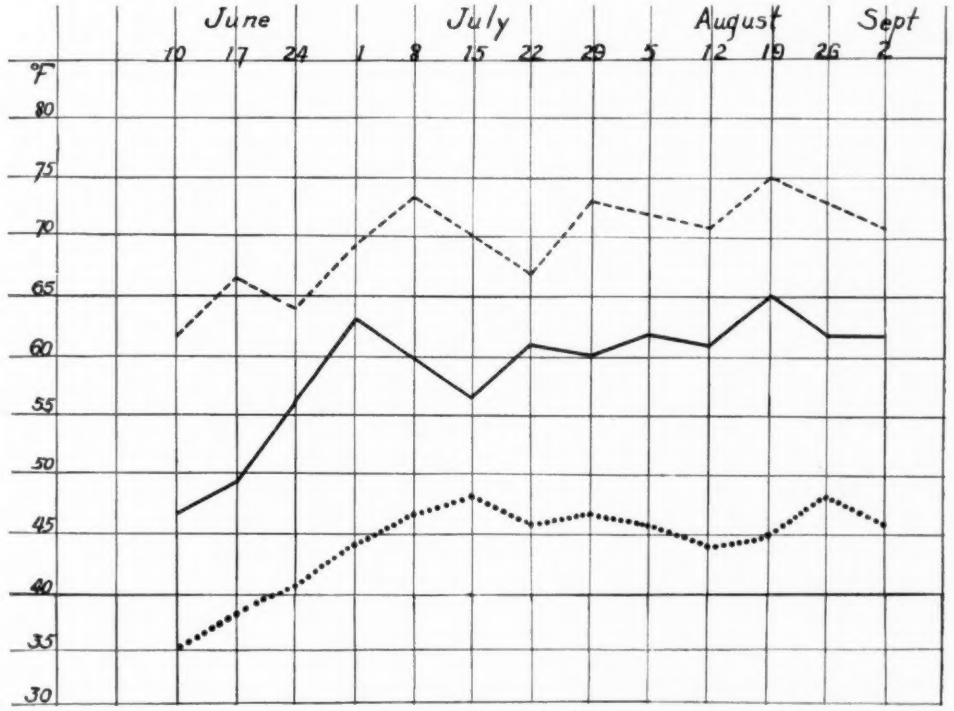


FIG. 10. Average soil temperature at 4 inches, by weeks, 1927-29; Alpine, 1927-30. Legend: Plains— — — —; Montane————; Alpine . . . .

The data were secured by means of thermographs. Day and night averages were obtained by adding the temperatures at the several hours between 6 A.M. and 6 P.M. and 4 A.M. respectively. The records extend from May 27 to September 2 over a period of four years. Other records, unless otherwise indicated, cover the same period.

Soil temperature likewise shows a marked decrease with increased altitude. The average daily soil temperatures at the several stations were 70, 59, and 44° F. for plains, montane, and alpine respectively. The average difference between the plains and montane station was 11°, and between the montane and alpine regions it was 15° (Fig. 10). The records were secured by means of soil thermographs, with the tubes buried at a depth of 4 inches. The results were obtained in the same manner as those for air temperature.

SATURATION DEFICIT

The records for the daily saturation deficit were secured in the following manner. Simultaneous temperature and relative humidity readings were made at the three main stations at various intervals during the summers of 1929 and 1930. The cog psychrometer and the hygrothermograph were used to secure the relative humidities. With these relative humidities the weight of a cubic foot of aqueous vapor at the different temperatures were secured from Table XII, Psychrometric Tables issued by the United States Department of Agriculture. The water deficits for the various days were averaged to secure the daily averages.

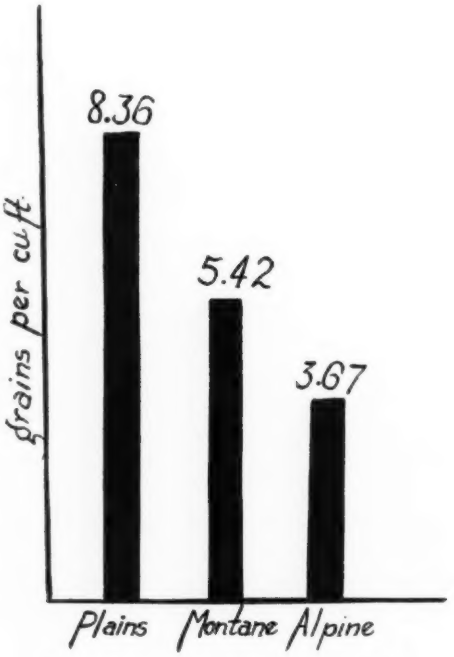


FIG. 11. Saturation deficit, 1930.

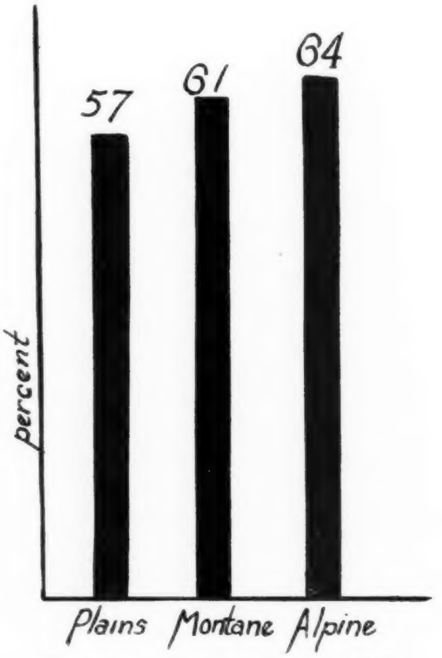


FIG. 12. Relative humidity, 1930.

The average daily saturation deficit of the air decreases with an increase in altitude (Fig. 11). There is a difference of 2.94 grains between the weight of vapor in a cubic foot of air on the plains and that at the montane station. A smaller difference, 1.76 grains, is found between the montane and alpine stations. The daily water deficit averages at the three main stations, plains, montane, and alpine, were 8.36, 5.42, and 3.67 grains respectively.

RELATIVE HUMIDITY

The average daily relative humidities increased only slightly with elevation, being 57% on the plains, 61% at the montane, and 64% at the alpine station. A difference of 4% exists between the plains and montane, and 3% between the montane and alpine (Fig. 11). During the night, when humidity is less efficient, it was higher on the plains, while during the day it was higher

in the alpine than at the other two stations. The records were secured by means of hygrothermographs, and the results obtained in the same manner as those for air temperature.

EVAPORATION

Evaporation was obtained by means of open surface and Piché evaporimeters and standardized white spherical atmometers mounted on jars. Both the evaporimeters and the atmometers, the latter run in duplicate, were set in the soil in such a manner that the evaporating surface was on an approximate level with the surrounding vegetation.

Evaporation decreased with altitude from the open surface and Piché evaporimeters (Fig. 13), while the results from the atmometers were irregular as regards the montane and alpine zones. In 1929 the average weekly atmometer losses were as follows: Plains, 326 c.c.; montane, 132; alpine, 175; summit, 165; while in 1930 the losses were: plains, 210; montane, 143; and alpine, 138.

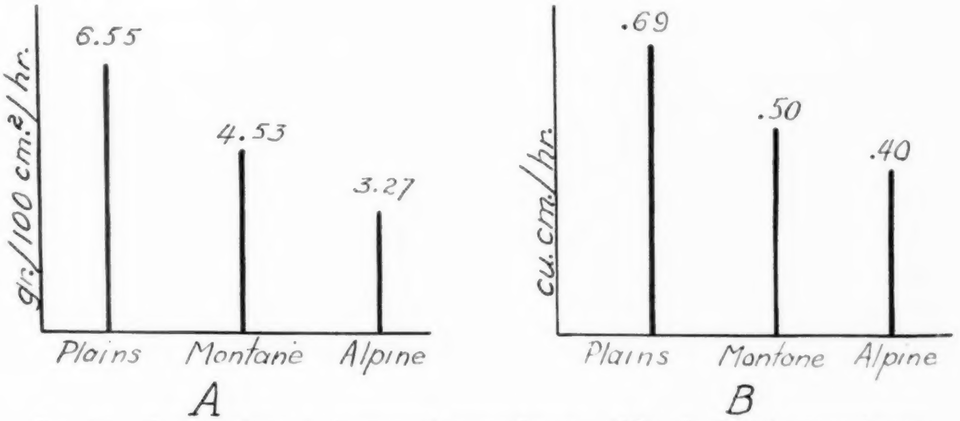


FIG. 13. Evaporation: A, improved evaporimeter, 1931; B, Piché evaporimeter, 1931.

WIND VELOCITY

The rate of wind movement is very dependent upon local topographic conditions, such as direction of mountains, and exposure. The average wind velocity records in miles per hour for the seasons of 1929-1930 show that the alpine station has twice as much wind as the plains, the summit slightly less than the alpine, and the montane the least (Fig. 14). The wind velocity in M.P.H. at the plains was 2.51, at the montane level 0.9, at the alpine station 5.45, and on the peak 4.4. Much of the wind movement in the alpine region occurred at night, while the greatest velocity on the plains occurred during the day.

RAINFALL

The average seasonal rainfall for 1929 and 1930 was greatest in the alpine region and smallest on the plains (Fig. 15). The summit has a lower rainfall

than the alpine region. The average precipitation in inches for the two seasons at the various stations was 9.87 for the plains, 14.36 for the montane, 18.04 for the alpine, and 15.38 for the peak. The average annual precipitation for nine years at three stations shows an increase in rainfall with altitude (Fig. 16). The averages are: Colorado Springs, 13.58; lower subalpine, 23.3; and subalpine, 24.67. The altitudes at the stations where the data were secured are: Colorado Springs, 6,100 feet; lower subalpine, 9,040 feet; and subalpine, 10,247 feet.

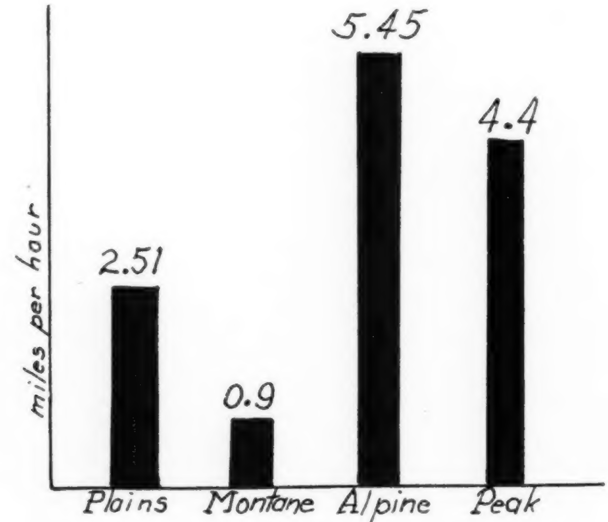
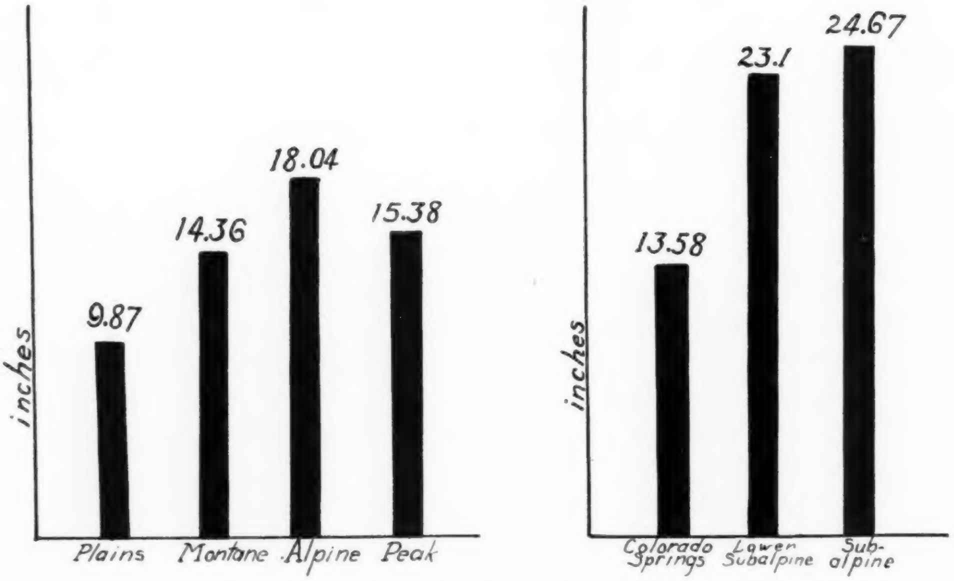


Fig. 14. Average wind movement, 1929-30.



Figs. 15-16. Average rainfall: May-September, 1929-30; annual, 1921-29.

HOLARD

The soil samples for determining water content were taken at the surface, at four inches, and at twelve inches, by means of a trowel. They were subjected to a heat of 90 to 100° C. for a period of 48 hours. Samples

TABLE III. *Holard, 1929.*

Levels	*Plains*	*Montane*	*Alpine*
Surface	3.49	10.15	21.19
4 inches	3.90	12.02	20.40
12 inches	4.82	11.09	16.47

were taken every Monday between June 10 and July 29, 1929. The soil from the alpine station contained twice as much soil moisture as that from the montane station, and four times as much as the soil from the plains (Table III). These values agree with those obtained in earlier work (Whitfield, 1928).

WILTING COEFFICIENT

Preliminary studies on the echard were made during the summer of 1930 at the three main stations. Sunflower seeds, which had been previously soaked for twenty-four hours, were planted in soils taken from the stations. The plants were allowed to wilt, and at the time of wilting holard determinations were made. The wilting coefficients of the soils at the different stations were: plains, 4.4; montane, 3.3; and alpine, 4.7. If we assume that the wilting coefficient is the practical expression for non-available moisture, judging by these results there is little variation in the echard at the different stations.

SOIL ACIDITY

Two determinations of the hydrogen-ion concentration at the three main stations were made in June and July, 1929. An alkaline soil exists at the

TABLE IV. *Average soil acidity determinations.*

Levels	*Plains*	*Montane*	*Alpine*
Surface	6.99	7.41	5.88
4 inches	6.39	7.41	5.59
12 inches	6.52	7.69	5.25

montane station. Soils were acid at the plains and alpine stations, the latter being more acid than the former (Table IV). The pH increases with depth in the acid soils. No direct measurements have been made, but observations indicate that the soil in the alpine region, in addition to being more acid than that of the lower regions, contains more humus and more worms.

ECOLOGICAL ANATOMY

The gross anatomy of the various climaxes has been briefly discussed under vegetation. The present observations have been confined to leaf structure and stomatal distribution of the plants in the montane, subalpine, and

alpine zones. The leaf section drawings were made by means of the Bausch and Lomb projection apparatus and camera lucida. E. S. Clements (1905) worked with native species of this region on the relation of leaf structure to physical factors. This is the most extensive work of its kind that has been done.

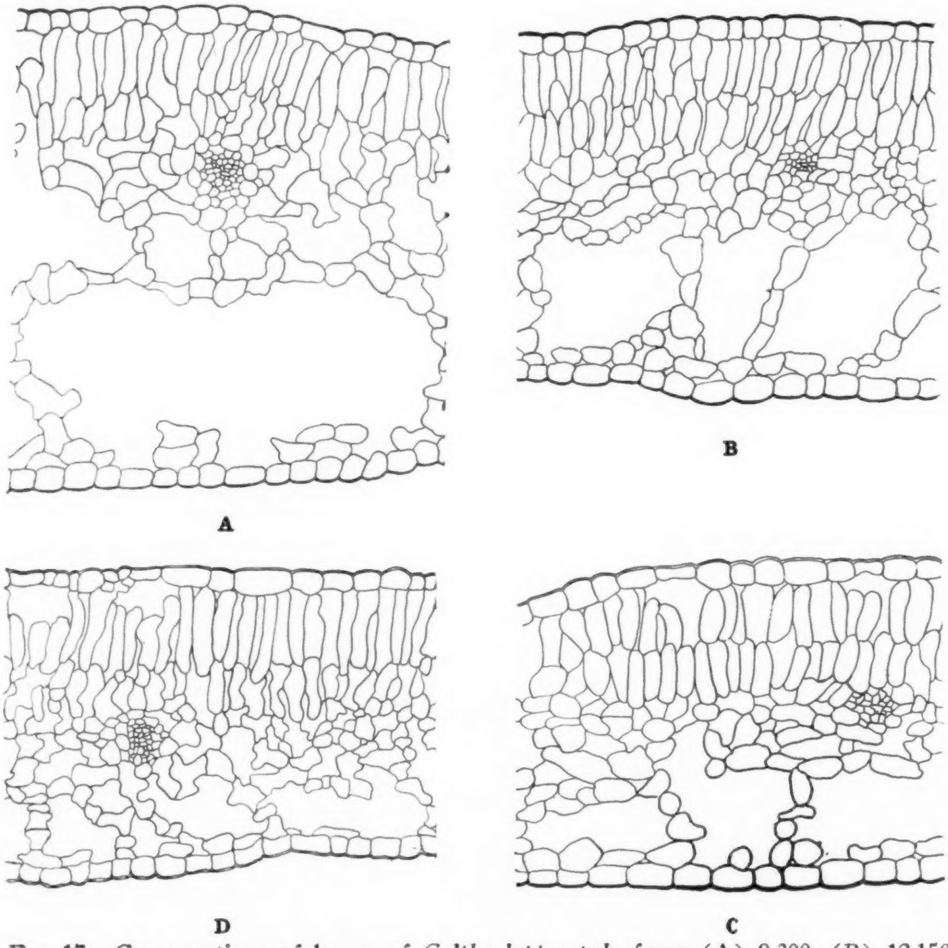


FIG. 17. Cross-sections of leaves of *Caltha leptosepala* from (A) 9,300, (B) 12,150 (wet), (C) 12,150 (dry), and (D) 13,500 feet.

LEAF STRUCTURE

With an increase of altitude and exposure the outer wall of the epidermis of the leaves becomes slightly thickened and tissue in the leaves becomes much more compact. Palisade increases, and the amount of air space decreases with altitude (Fig. 17, Table V). The plants in the alpine tundra were fully exposed; those in the subalpine were shaded during the first part of the morning and late afternoon. Sections made from fully exposed leaves showed that *Chamaenerium angustifolium*, *Dasyphora fruticosa*, *Mertensia sibirica*, and *Populus tremuloides* were, in general, similar to Caltha in their responses to habitat (Fig. 18).

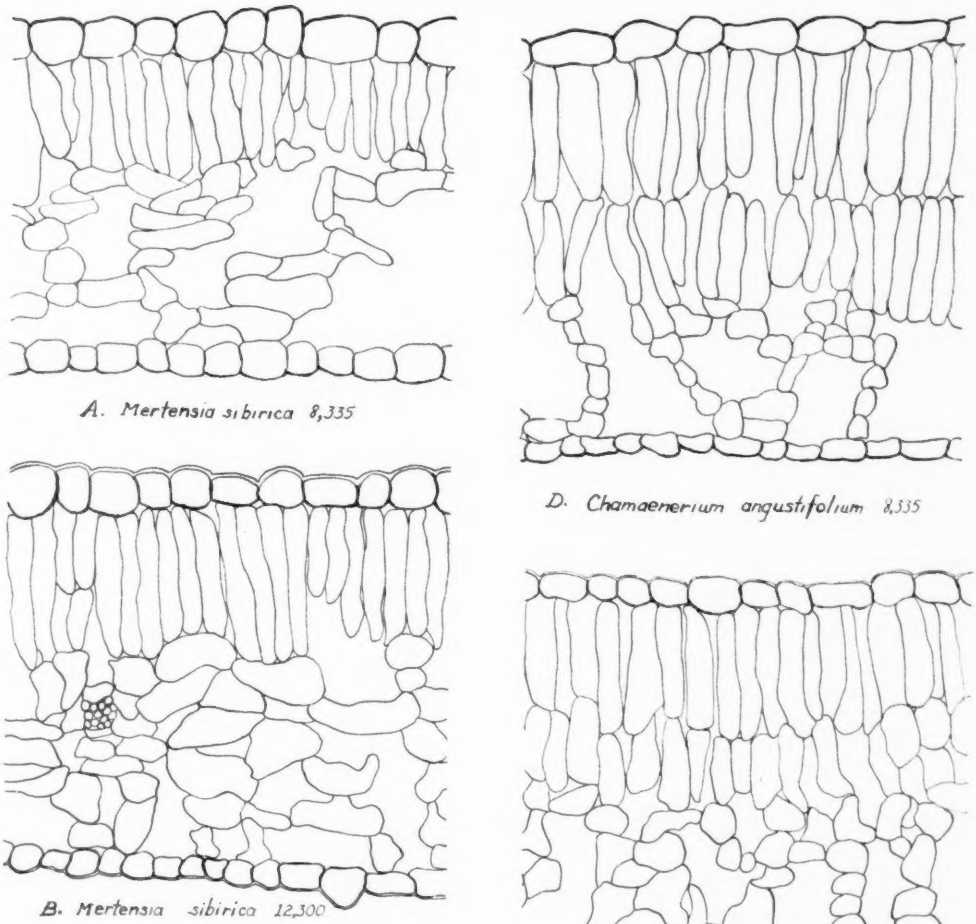


FIG. 18. Cross-sections of leaves. *A, Mertensia sibirica*, 8,335; *B, M. sibirica*, 12,300; *C, Populus tremuloides*, 11,500; *D, Chamaenerium angustifolium*, 8,335; *E, C. angustifolium*, 10,200; *F, Dasyphora fruticosa*, 12,150.

Table V. *Table of measurements taken from cross-sections of leaves shown in Fig. 17.*

Station	Thickness of leaf, microns	Palisade		Sponge		Air space, per cent	Average thickness of epidermis, microns
		Rows of cells	Length of cells, microns	No. of cells	Diam. of cells, microns		
9,300.....	555	1	75	54	38	100	3.0
12,150 wet.	450	2	67	68	33	52	3.3
12,150 dry.	367	2	67	68	35	29	4.8
13,500.....	350	2	90	78	25	26	4.8

Stomatal Distribution

The results of stomatal counts on montane and alpine herbaceous species indicate, in general, that montane species have more stomata on the lower epidermis than on the upper (Table VI). Typical sun species have nearly twice as many stomata as typical shade species per unit area. Individuals of the same species growing in the sun and shade have only slightly higher numbers in the sun.

Alpine species have stomata approximately equally distributed on the two surfaces. Many species, for instance those of Artemisia, Caltha, Claytonia, and Mertensia, have more stomata on the upper surface; others, Senecio, Thalictrum, and Veronica, for example, have more on the lower epidermis. Montane and subalpine species growing in the alpine tundra show approximately the same number of stomata per unit area as they have in the lower region. Alpine species show more stomata per unit of area than montane shade species, but montane sun species, although having about the same number on the upper epidermis as the alpine species, have more stomata on the lower epidermis.

FUNCTION

Transpiration

Transpiration is of ecological importance (Clements and Goldsmith, 1924; Clements and Weaver, 1924). Clements, Goldsmith, Weaver, and Lutjeharms made numerous transpiration studies in the Pike's Peak region during the years of 1917-1923. These workers confined their attention primarily to edaphic studies in the plains and montane formations.

Recent transpiration studies have been conducted in all the climatic zones of the Pike's Peak region (Figs. 22, 23). Galvanized iron containers approximately six inches wide and 12 inches deep were used. All containers were equipped with valves and were regularly aerated. A glass tube in the containers permitted watering when necessary. Native species as well as corn, wheat, and sunflowers were employed as phytometers. When native species

were used, 75 to 100 plants were potted with native soil in containers with as little disturbance as possible, and allowed time for adjustment. When corn, wheat, or sunflowers were used, the seeds, previously soaked for 24 hours, were planted in uniformly mixed soil in containers and allowed to develop the first set of leaves. All the plants were sealed, weighed, and placed on a revolving table (Figs. 19, 20). After three or four days they were

TABLE VI. *Stomatal Distribution*

MONTANE SPECIES

Sun	Upper	Lower
Allium cernuum	5.4	7.9
Castilleia miniata	8.3	12.7
Chamaenerium angustifolium	0.0	44.9
Erigeron macranthus	19.9	13.9
Geranium caespitosum	17.0	19.9
Senecio fendleri	13.3	24.8
Average distribution	10.7	20.9

Shade	Upper	Lower
Allium cernuum	5.4	4.8
Campanula rotundifolia	6.6	13.4
Castilleia minuiata	6.3	11.8
Erigeron glabellus	5.0	9.4
Gentiana amarella	0.0	10.6
Geranium caespitosum (part shade)	11.7	16.1
Geranium richardsoni	1.0	15.1
Mertensia pratensis	4.8	7.2
Senecio cernuus (part shade)	5.7	9.4
Senecio cernuus	3.3	7.5
Thalictrum fendleri	0.0	15.7
Average distribution	4.5	11.0

SPECIES FOUND IN BOTH MONTANE AND ALPINE REGIONS

	Montane		*Alpine*	
	Upper	Lower	Upper	Lower
Campanula rotundifolia	8.8	12.3	7.1	14.4
Gentiana amarella	0.0	17.4	2.6	13.7
Mertensia sibirica	0.0	20.8 (shade)	0.0	22.2
Average distribution	2.9	16.8	3.2	16.8

ALPINE TUNDRA SPECIES

	Upper	Lower
Antennaria alpina	11.6	6.8
Artemisia pattersoni	14.1	6.8
Artemisia scopulorum	8.7	5.4
Caltha leptosepala	12.5	7.5
Castilleia p. occidentalis	14.1	12.2
Claytonia megarrhiza	6.8	4.7
Erigeron uniflorus	18.5	10.5
Gentiana frigida	2.3	6.7
Mertensia alpina	19.7	16.3
Pentstemon halli	14.9	14.3
Saxifraga nivalis	21.6	21.6
Senecio a. croceus	10.9	11.4
Senecio fremonti	8.5	9.5
Senecio taraxacoides	7.3	10.0
Sieversia turbinata	11.0	7.9
Solidago nana	14.4	15.2
Thalictrum alpinum	0.0	28.7
Veronica alpina	10.7	17.2
Average distribution	11.5	11.8

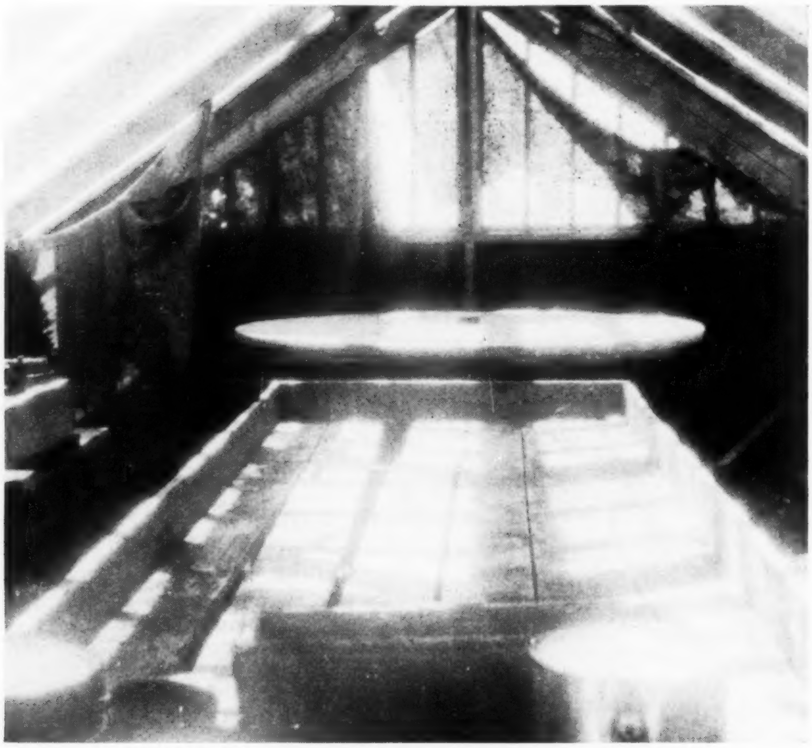


FIG. 19. Revolving table used for standardization purposes.

re-weighed. The standardized plants, which gave similar results under neutral conditions, were divided into groups and placed in the climatic stations. Short period phytometers, for three or four days, were used.

The average transpiration of *Helianthus annuus* decreases with an increase in altitude. The average loss on the plains was 42 grams, approximately four times as much as on the summit (Fig. 21). *Helianthus annuus* was used as a standard plant in all transpiration experiments. Results obtained from *Mertensia sibirica* and *Mertensia alpina,* natives from the montane and alpine formations respectively, indicate climatic differences similar to those shown by Helianthus, namely a decrease in transpiration with increased altitude. Average daily transpiration of *Mertensia sibirica* at three stations was: plains, 34 grams; montane, 31; and alpine, 17 (Fig. 24). *Mertensia alpina* showed average daily losses of 28, 22, and 16 grams respectively at the three stations (Fig. 25).

Clements and Goldsmith (1924) found, from data recorded at three stations, plains, montane, and subalpine, that the subalpine plants had the lowest transpiration.

OSMOTIC VALUES

The osmotic concentrations of the sap of species are of ecological importance. Preliminary studies in this field were made during 1930. Osmotic

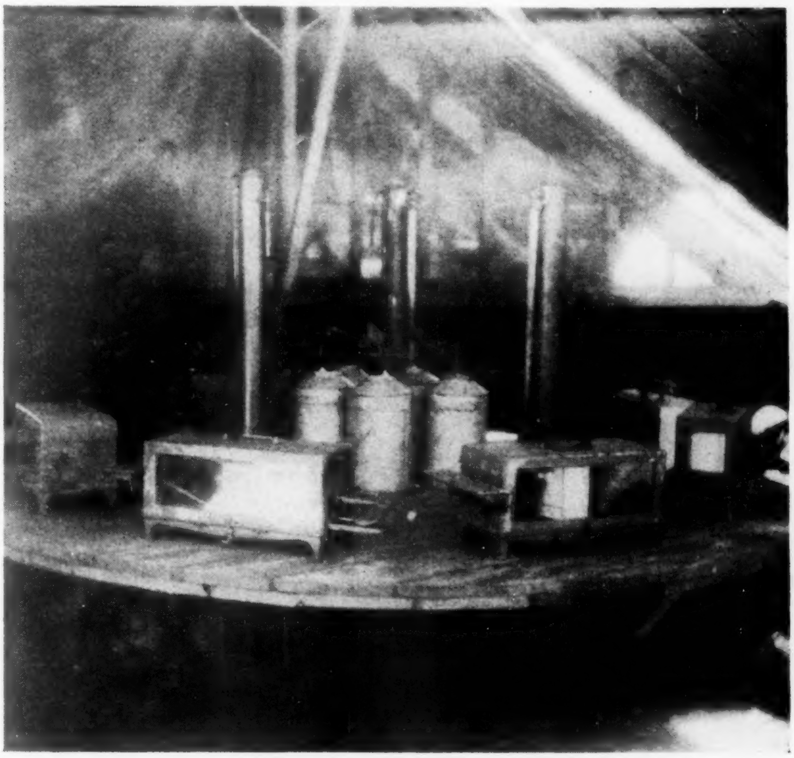


FIG. 20. Standardization of phytometers and instruments.

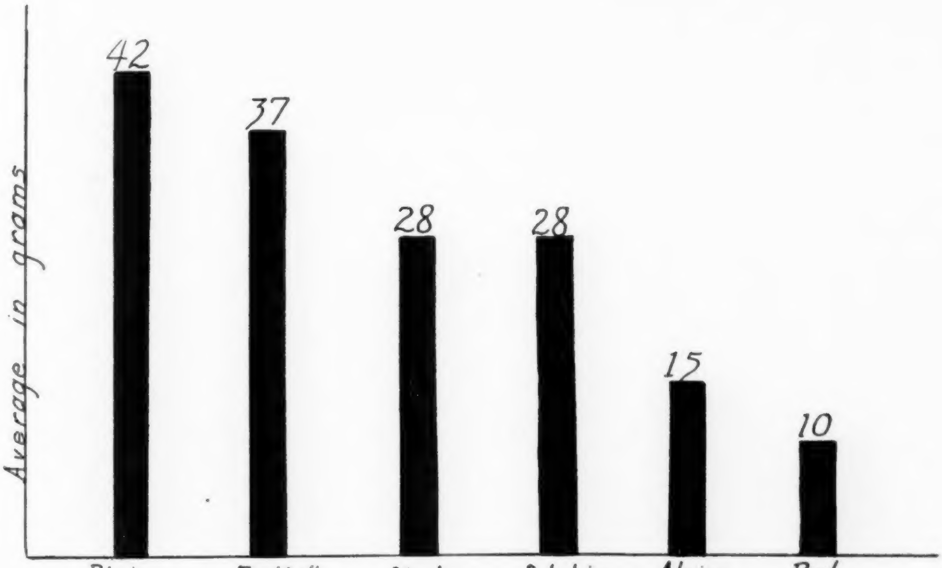


FIG. 21. Transpiration: *Helianthus annus;* July, 1930.

pressures were determined by means of the freezing point depression according to the method of H. Walter, modified from that of Gortner and Harris (1914).

In general, sap concentration increases with altitude, and osmotic values are higher during the winter season than in late summer (Table VII). These results agree with those of Goldsmith and Smith (1926).

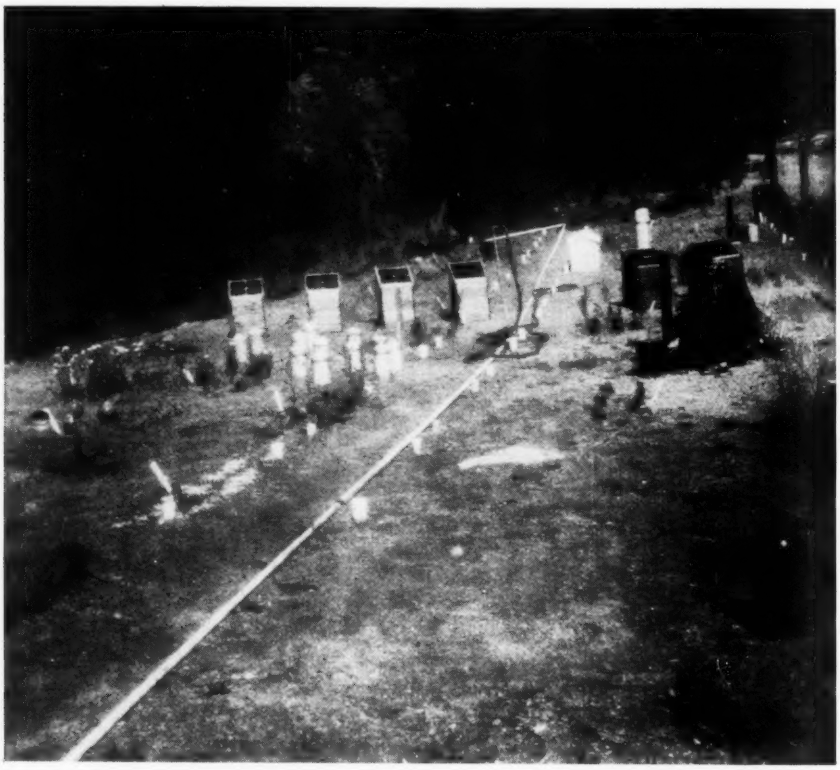


FIG. 22. Phytometers and instruments at montane station.

TABLE VII. *Osmotic pressures.*

Species	Date	6,300	8,330	9,200
Pseudotsuga mucronata	Dec. 26	31.85 (6,500)	33.18	42.07
Pinus ponderosa	Dec. 26	32.71	33.88	33.84
Juniperus communis	Dec. 26	.....	36.24	39.25
Arctostaphylus uva-ursi	Dec. 26	.....	34.26	39.21
Yucca glauca	Dec. 26	27.25	25.49	.....
Pinus edulis				
Old leaves	Aug. 17	28.29		
Old leaves	Dec. 26	41.71		
New leaves	Aug. 17	22.18		
New leaves	Dec. 26	35.51		
Juniperus monosperma	Aug. 17	23.62		
	Dec. 26	37.25		

FIG. 23. Phytometers and instruments at alpine station.

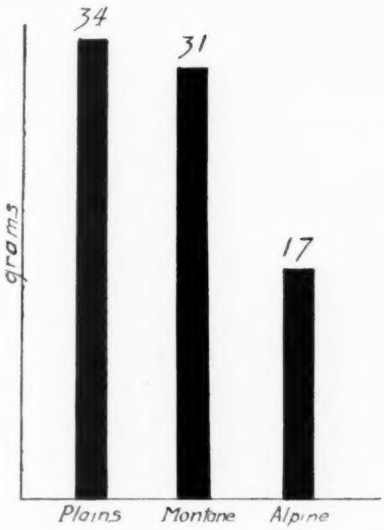


FIG. 24. Transpiration: *Mertensia sibirica;* July, 1930.

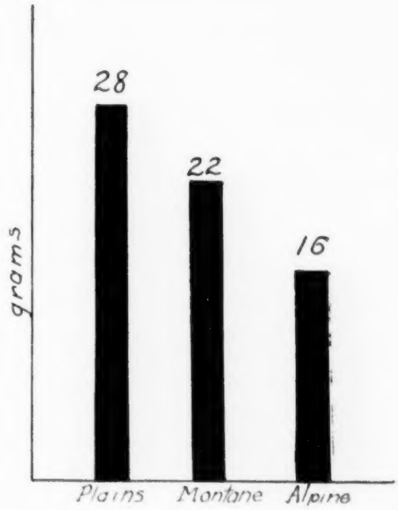


FIG. 25. Transpiration: *Mertensia alpina;* July, 1930.

Osmotic concentrations of species in the alpine tundra are not high. Caltha from the alpine tundra had osmotic values of 13.7 and 11.7 (Fig. 17, B, C), Caltha of similar size taken from the subalpine region showed values of 12.6 and 12.4. Osmotic values of some other alpine plants, measured in atmospheres of pressure, are: *Mertensia alpina*, 10.0; *Androsace chamaejasme*, 12.4; *Sieversia turbinata*, 18.2; and *Polemonium confertum*, 13.1. Species in the alpine tundra have higher values than shade individuals of the same species in the montane zone, but species growing in the sun in the montane region have higher values than individuals of the same species in the alpine meadows (H. Walter, 1931).

SUMMARY AND CORRELATION

1. The vegetation of the Pike's Peak region consists principally of the Plains, Montane, Subalpine, and Alpine Tundra climaxes of these continental formations.
2. *Bouteloua gracilis*, *Sporobolus cryptandrus*, and *Stipa comata* are the conspicuous dominants of the plains; *Pinus ponderosa* and *Pseudotsuga mucronata* dominate the montane; *Picea engelmanni*, *Populus tremuloides*, and *Pinus aristata* are most important in the subalpine; and *Elyna bellardi*, *Carex rupestris*, *Artemisia scopulorum*, *Polygonum bistorta;* and *Sieversia turbinata* are the most abundant alpine species.
3. The following factors decrease with an increase in altitude: day and night air temperature, soil temperature, and moisture saturation deficit.
4. Rainfall, relative humidity, and holard rise with an increase in altitude.
5. Wind movement is lowest in the montane, higher in the plains, and highest in the alpine tundra.
6. Evaporation is lowest in the montane, higher in the alpine tundra, and highest on the plains.
7. There is little difference in the echard in the climax soils at the various stations.
8. Soil acidity is highest in the alpine climax and lowest in the plains, the montane being slightly alkaline.
9. A comparison of the physical factors of the four main climaxes show that the plains is characterized by high day and night air temperatures, a high soil temperature, saturation deficit, evaporation, and wind movement, a low rainfall and holard, and a long growing season. These factors, especially the high water saturation deficit and wind movement, and low rainfall, account, at least in part, for the xerophytic character of the vegetation and its high transpiration.
10. The montane zone, with lower air and soil temperatures, lower water saturation deficit, lower evaporation, lower wind movement, higher rain-

fall, higher relative humidity, and higher holard has a more mesophytic vegetation with a lower transpiration.

11. The subalpine is distinguished by slightly lower temperatures and water saturation deficit than the montane, higher rainfall, wind movement and evaporation. Transpiration is lower here than in the montane.
12. The alpine tundra is characterized by low air and soil temperatures, water saturation deficits, and evaporation, and by high rainfall, wind movement, and holard. Transpiration and osmotic pressures are comparatively low. The compact tissues, with several rows of palisade cells and relatively more stomata on the upper surface of leaves indicate that the alpine vegetation is constructed for rapid functional activities, namely transpiration, photo-synthesis, and respiration. It has been shown (Whitfield, 1928) on the basis of the amount of photosynthate produced, that, with all other factors equal there is greater functional activity in the alpine tundra than in the other climaxes. Alpine dwarfing appears to be partly a result of low air and soil temperatures, which limit continuous and rapid activity.

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A STUDY OF SOIL CHANGES ASSOCIATED WITH THE TRANSITION FROM FERTILE HARDWOOD FOREST LAND TO PASTURE TYPES OF DECREASING FERTILITY

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* This investigation was carried on while the author held the University Fellowship in Agriculture in the Agronomy Department of Cornell University. The results were presented to the Graduate School of that University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

CONTENTS

A STUDY OF SOIL CHANGES ASSOCIATED WITH THE TRANSITION FROM FERTILE HARDWOOD FOREST LAND TO PASTURE TYPES OF DECREASING FERTILITY

In the eastern United States, past records show that the fertility of the pasture area when first it was cleared of the virgin forest was very high. But at the present time evidence is accumulating to show a decrease in the amount and the value of pasture forage. The specific problems considered in this publication are concerned with some aspects of this decrease in fertility as demonstrated in the pastures of New York State.

The Cornell Station has already carried on a number of studies in pasture improvement. Montgomery (18) investigated the possibility of using lime and phosphate in combination with re-seeding. The development of pastures by plowing and planting with mixtures of timothy, clover, and red-top has been reported by Wiggans (25). Under conditions of average fertility, he found this treatment resulted in a final pasture consisting largely of blue grass and orchard grass, with varying amounts of clover. Later Wiggins (26) studied the effect of fertilizers, lime and manure, seeding, and cultural treatments on the development of pastures in three areas representing differing states of productivity. The locations were chosen to show: (1), the most depleted soils; (2) those that were moderately unproductive; and (3) the high-grade pasture soils of the state. Under all three conditions of fertility, the application of acid phosphate resulted in increases amounting approximately to 20 per cent in the herbage produced. Lime, like phosphate, gave a positive response on the plots of all groups. Nitrate of soda, on the other hand, while showing a definite increase on the moderately unproductive land, appeared to cause a decrease in the development of clover. A large response was obtained from applying manure to the poorest areas. After a lapse of several years it was observed that neither ploughing nor re-seeding had produced a positive result in any of the areas studied.

Recently Cooper (7), Cooper, Wilson, and Barron (9), and Cooper and Wilson (8) have carried on an extensive series of investigations of the pasture problems of the northeastern states. As the result of their field studies they suggest that a more or less definite type of pasture plant succession has occurred in this section of the country. They believe that when the forest trees were first cleared from the land there was sufficient accumulated fertility in nearly every well-drained soil type to support a good growth of Kentucky blue grass and white clover. The period of time during which blue grass persisted was determined largely by two factors: climatic conditions, and the inherent fertility of the soil. They further suggest that varied soil conditions, due to

differing types of forest cover, may pre-determine the later relationship of pasture plants. Where the forest was composed of pine, spruce, hemlock, grey birch, and red maple, a rapid decrease of fertility may be expected; the Kentucky blue grass of the first pasture period will be succeeded by Rhode Island bent or red-top, and these in turn by sweet vernal and poverty grass. The final succession, on the most depleted areas, may be cinquefoil, moss, ferns, and pine trees. On the other hand, soils which originally carried a typical hardwood cover of hickory, ash, beech, elm, and sugar maple may be expected to maintain a higher level of fertility, and to retain their Kentucky blue grass pasture for a considerably longer time.

Cooper and Wilson (8) have determined the composition of the ash of pasture plants from some forty-five of the more common plant associations, and as a result of this work have developed a most stimulating theory as to the manner of absorption of ions by the plants. They have found that in general the samples taken from productive soils contain a large amount of the elements which form strong ions, while those taken from unproductive soils have a relatively low ash content, and are comparatively high in the elements which form weak ions. They have therefore suggested that there is a correlation between the standard electrode potentials of the elements and the amounts of the various minerals in the ash of the plant. They have further suggested that plants grown on fertile soil are often intolerant of shade and require a large amount of radiant energy for the best growth, and therefore are likely to synthesize organic compounds of high forage value; while plants grown on poor soils are frequently tolerant of shade, and are of relatively low food value.

EXPERIMENTAL WORK

Scope of Problem

The purpose of this study is to extend the work of Cooper and Wilson (8) by an investigation of the soils producing the forage plants considered in their papers. It would appear to be of interest to determine whether the same difference which they found in the mineral content of the ash from grasses of the high-yielding and low-yielding pasture groups is clearly reflected in the state of fertility of the soils on which these grasses grew. In planning this investigation the writer was favored with the cordial coöperation of Professor H. P. Cooper, and through access to his excellent field notes was enabled to collect profile soil samples from exactly the same pasture areas from which Cooper and Wilson had gathered their plant material.

It is believed that nearly all the pasture regions of the northeastern states were originally covered by forest. The initial fertility which this pasture land possessed was therefore the result of the decomposition of the forest litter through many years. The observations of members of the Agronomy Department of Cornell University would indicate that the most fertile pas-

tures are those which formerly supported a growth of the best type of hardwood forest. In order to have a standard of comparison which would show any soil changes which had occurred in the poorer pasture soils, it had been decided to include a group of hardwood forest soils in the present study. These forest soils will as far as possible be located on the same soil series as the better Kentucky blue grass pastures.

The soils to be considered in this investigation, then, will comprise: a group of forest soils; groups of pasture soils of the following grass types (1) Kentucky blue grass *(Poa pratensis)*, (2) Rhode Island bent *(Agrostis tenuis)*, (3) sweet vernal grass *(Anthoxanthemum odoratum)*, (4) poverty grass *(Danthonia spicata)*; and a group selected from pastures displaying heavy intrusions of moss and fern. In choosing the forested areas, it of course would have been desirable to have examined virgin hardwood forest land. But this was impossible to find adjacent to the pasture areas which Cooper had investigated. There were, however, a number of second growth hardwood forest areas available, where the tree growth was excellent and where the humus layer could be classed as a typical earthworm mull. Such land represents some change from virgin forest soil, but in many cases pastures were first established on similar transitional soil after its forest cover had been removed. The soils of the six forest areas selected were expected to supply a standard against which the soil changes caused by pasturing might be measured.

Reference has previously been made to the theory advanced by Cooper, Wilson, and Barron (9) that a rather definite succession of pasture plants has tended to take possession of the land as its fertility is reduced from a high level. Careful field studies have developed considerable evidence in support of this theory. For the purpose of the present investigation, however, it is not essential that each of the poorer areas should have passed through all the stages of pasture grass succession. If the level of fertility is the determing factor in the dominance of each type of grass, the study of a series of pasture areas in which the typical grasses are in the ascendancy should give information of value.

The location of the areas chosen for investigation is given in Table I. Since Cooper had worked only on pastures, it was necessary for the writer to select the groups illustrative not only of forest soils, but also of moss and fern land. The balance of the samples, however, were collected from the identical pasture areas which Cooper and Wilson considered most typical of the four grass associations. Under each set of samples, the state of productivity has been indicated. It will be seen that the growth made on the hardwood forest soils and the Kentucky blue grass pastures was uniformly good. More variation occurred in the condition of the Rhode Island bent pastures, which ranged from good to very poor. Only three of the areas supported a sufficiently large amount of sweet vernal grass to make it possible to consider this grass the dominant cover. These three pastures were relatively poor.

All the pure poverty grass pastures were also poor. Four samples collected from Wooster and Volusia soils had the same type of growth—a relatively thin forage cover, consisting of a sparse sod of poverty grass. Two additional samples, Nos. 22 and 23, on Ontario loam, displayed a different type of development. Possibly Sample No. 22 should be classed as a transitional type, as it came from a run-down Canada blue grass pasture, with heavy intrusions of poverty grass. Sample No. 23 had present no other grass than poverty, but the major growth on this area consisted of weeds and small shrubs. These two are the only samples where there can be a question of the dominance of the typical grass. All the moss and fern samples were taken from portions of pastures where practically all grass had been crowded out by moss, fern, or a combination of the two.

The soil classification was taken from the U. S. Soil Survey maps, and in every case has been confirmed by local examinations of several portions of the pasture.

It will be seen that the forest and Kentucky blue grass soils include some of the best soil types found in the central portion of New York state, such as Ontario and Genesee loams, while the Wooster soils are rated as being of moderate productivity. A few representatives of the poorer soil series are found among the Rhode Island bent, sweet vernal, and poverty grass pastures, but here again the majority of the samples were taken on Ontario or Wooster soils. The moss and fern pasture soils are a new series, recently classified, so less is known as to their general agricultural value.

In Table I an attempt has been made to estimate the tree growth associated with each pasture soil. In the case of the forest areas, this was done by examination of the second growth as well as of the surviving trees and stumps remaining from the virgin forest. In the case of the pastures, both observations of adjacent trees, and such information as could be obtained in the field were used by Cooper and by the writer in constructing the estimate.

Numerous ecological studies of plant succession have shown that a change in environmental conditions may notably alter the typical tree and plant growth. Hence the writer hesitates to claim that the estimates made here represent accurately the original forest stand. On the basis of the present adjoining trees, however, it may be suggested that on the forest areas considered, as well as on the Kentucky blue grass soils, the best type of hardwoods have predominated. This has been largely true of the Rhode Island bent pastures, but part of them appear to have supported a growth that included trees less desirable from the point of view of soil fertility, such as hemlocks and pines. There is evidence that pine and hemlock have been present on some of the sweet vernal and the poverty grass pastures, as well as on most of the moss and fern land.

Plan of Field and Laboratory Studies

The field and laboratory work carried out on the samples described was planned with the intention of giving a picture of the major physical, chemical, and bacteriological differences between the various groups of forest and pasture associations from which they had been taken. The physical studies embraced: (1) studies of the soil profile in the field; (2) determinations of the permeability of the soil in the field to a head of 10 cm. of pure water, according to the method of Burger (4); (3) the determination of specific gravity, pore space, and air space, by the cylinder method of Burger (4); (4) physical analyses for colloids and clay by the hydrometer method of Bouyoucos (1). The bacteriological work consisted of the determination: (1) of the amounts of nitrates and ammonia formed from the soil's own nitrogen after a five week's storage period; (2) of the number of azotobacters, found by Winogradsky's (26) molded plate culture method, and the dilution method in Ashby's solution; (3) of the presence or absence of legume organisms as shown by the inoculation of legume plants grown in sterile soil with soil suspensions. The choice of the chemical work which would best reveal the state of fertility of the soils of the different plant associations brought up a number of possibilities. The writer (22) showed, several years ago in California, that the level of nutrients present in the soil solution of a group of cultivated soils when kept under controlled conditions gave an excellent picture of the inherent crop producing power of these soils. Such a series of observations should be made at periodic intervals throughout the growing season, however, and this was manifestly impossible for a single investigator, working on some thirty-four areas.

Cooper and Wilson (8) have suggested that the cations held in the soil's colloidal complex give a relative measure of the amount and rate of supply of the important mineral nutrients furnished to pasture plants. In support of this idea Menchikowsky and Ravikovitch (16) have reached the conclusion that, in highly mineralized soils, the composition of the soil solution relatively conforms to the composition of the replaceable bases in the soil's colloidal complex, and to a certain degree reflects the character of this complex. The nutrition of the plant, therefore, will be very directly affected by the replaceable bases present in the soil, and on the resultant effect of these bases on the soil solution from which, it is believed, the plant is nourished.

If we grant the soundness of these conclusions, it appears logical to go a step further. Under humid conditions of moderate rainfall, it is evident that the replaceable bases of the soil must be replenished from the total reserve supply of minerals present in it, as these minerals come into solution in excess rainfall. Though the soil is a complex mixture of numerous chemical components, ready to enter into reaction both in the solid and in the liquid phases, there is every reason to believe that the usual mass law relationships will

apply. That is to say, the rate, or speed, of a chemical reaction is proportional to the active masses of the reacting substances present at the time the reaction occurs. When chemical equilibrium is established it is due to opposing reaction velocities neutralizing one another. The writer therefore believes that the state of saturation of the colloidal complex of the soil with bases will depend on the active masses of these bases furnished by the soil minerals. In a soil which has arrived at a relatively constant reduced state of fertility, it is probable that the supply of nutritive bases furnished by the soil will be influenced by the total reserve remaining after leaching with rain and the removal of nutrients in forage. Since a considerable number of the soils of the poorer pasture groups included in the present investigation were probably in a low state of fertility, it was decided to determine the total nitrogen, the total carbon, the carbon nitrogen ratio, the total calcium, and the total phosphorus. The soil reaction was always determined by the quinhydrone electrode on the fresh samples as soon as they reached the laboratory. In order to have some indication of the probable availability of nutrients in the soils, all the samples were tested for available phosphorus, by the Illinois rapid test, essentially as given by Bray (2). The majority of them were tested for available lime, phosphates, and potash by the use of a pure culture of Azotobacter, and Winogradsky's molded plate culture method.

PHYSICAL STUDIES

The Soil Profile

On each forest and pasture area a series of preliminary examinations was made to determine the typical profile which could be considered characteristic of the location. A careful excavation was then made, through the A and B horizons, and down to the relatively unchanged subsoil which has been designated as the C horizon. As the material from which all the soils were derived was of glacial origin, it is possibly a misnomer to speak of this lower subsoil as the C horizon, since this term is usually applied to the parent material from which the soil has originated. In all cases there was a notable change in the physical appearance of this lower subsoil, indicating a relatively unaltered state of this portion of the profile, and for this reason the term C has been used. The selection of the forest land to be examined depended on its possessing a typical earthworm mull as defined by Müller (19) in his classic work on humus formations, as well as an excellent stand of the best type of hardwood trees. The horizon designations used throughout the study are those of Glinka (12), which are now generally employed in soil profile nomenclature in the United States. According to Glinka's classification, the letter A is employed to designate the eluvial horizon, that is, the entire horizon from which, in the process of weathering, solutes and colloidal material have been removed by leaching. The zone of concentration below this is called the B

horizon, and the letter C is used to indicate the still lower parent material. In studying the profile, it is customary, when there is a change either of color or texture in any horizon, to subdivide it into A_1, A_2, etc. Romell and Heiberg (20) have recently published an excellent discussion of the humus layers found in forest soils of the northeastern states, and have made careful comparisons of their classifications with European usage.

The depths of the A and B profiles in centimeters are given in Table IV. In the better pastures, that is, those supporting Kentucky blue grass and Rhode Island bent, the root growth filled these two horizons quite completely, and even penetrated into the lower subsoil, or C horizon. In the poorer pastures, this was not the case. The root growth of the sweet vernal, poverty grass, and moss and fern formed a dense, compact mat on the surface, with only a small root-growth extending down into the B horizon.

The sum of the depths of the humified A and B horizons gives a measure of the area available for root growth, and is especially important, since the better pasture grasses used all of this root zone, while the poorer occupied only part of it. The following summary of the mean depths of the A and B horizons of each soil group indicates that the forest soils and those of the two better pasture types had a significantly deeper root feeding zone than did the sweet vernal, poverty grass, and moss and fern soils.

SUMMARY OF DEPTHS OF A AND B HORIZONS, IN CENTIMETERS

	Mean Depth	*P. E. of Mean*
Forest soils	44.1	±4.80
Blue grass soils	48.0	±4.10
Rhode Island bent soils	40.0	±2.16
Sweet vernal soils	31.0	±1.75
Poverty grass soils	36.0	±1.38
Moss and fern soils	32.0	±2.29

The next fact of interest brought out by the profile studies was one related to the nature and distribution of the organic matter. In all the forest soils examined, there was a relatively small amount of undecomposed litter present. This has been pointed out by Müller (19) as one of the characteristics of the best mull formations. He, like Darwin (10), is inclined to trace this rapid disappearance of the fallen leaves to the activities of earthworms, though he also suggests that insects may be a considerable factor in the disintegration of the leaf material. The A horizon of each of the forest areas was a fine black mull which gave every visual evidence of a high content of decomposed organic matter. The B horizon was lighter in color, but here also there was an appreciable amount of humified material.

The appearance of the A and B horizons of the Kentucky blue grass soils were very similar to those of the forest soils, though in both layers they were slightly lighter in color. The Rhode Island bent soils were also lighter in tint than those of the forest; they showed the same evidence of a moderate content of decomposed organic matter that was noted in the blue grass sam-

ples. It is believed that the determination of the organic carbon in these three groups of soils gives a fairly correct expression of the disintegrated organic material present in them. It will be seen in Table IV that the forest soils showed a mean content of 6.65% of organic carbon in the A horizons, and that the blue grass and Rhode Island bent soils both contained 4.90%.

In the sweet vernal pastures the soils were grey in color, in contrast to the blackish brown of the groups just discussed. There was a tendency for the dead grass material to form a dry mat on the surface of the soil, instead of combining with the soil mass and decomposing normally. This effect of the accumulation of plant residues was greatly intensified in part of the poverty grass and the moss and fern areas. In three of the poverty grass pastures sampled, this organic matter formed a layer about three centimeters thick, which seemed to have the effect of practically choking out grass growth, and of encouraging the development of small mosses. The determination of the organic carbon in this surface accumulation of plant residues and soil showed a content ranging from 14% to 15%. The same general condition of plant residues was found to be a factor in part of the moss and fern land. Nitrification studies, to be discussed later, indicate that most of this organic accumulation is of relatively low availability, though the determinations of total nitrogen show that it has an appreciable nitrogen content. These observations suggest that one factor associated with a poor growth of grass on the less fertile pastures is the locking up of nutrients in the undecomposed plant remains.

Determination of Physical Factors

Burger (4, 5), working in Switzerland, has carried out a number of investigations in which he has compared the physical state of forest, pasture, and meadow soils. The forests studied by him have embraced a wide range of silvicultural conditions, while the pastures with which the forest lands were contrasted varied appreciably in fertility. The methods he employed in his investigations called for the use of two types of cylinder. One, 20 cm. in height and 100 sq. cm. in area, was used to determine the permeability of soil to a head of 10 cm. of pure water. The cylinder was driven into the ground to a depth of 10 cm., and then filled to the top with 10 cm. of distilled water. The time taken by this water to pass completely into the soil was noted with a stop watch. This simple procedure has given Burger information of value in studying the probable run-off of water from forested and from agricultural land. He found that forest soils of good mixed tree growth showed a greater permeability to water than did pastures, or even agricultural land recently plowed.

The second type of cylinder used by Burger was 10 cm. in height, and 100 sq. cm. in area, and hence had a volume of 1 liter. It was fitted, top and bottom, with covers. After small irregularities on the surface of the ground

were smoothed away, it was driven completely into the soil. To avoid compacting the soil surface, a driving ring 2 to 3 cm. high was used. The driving ring was removed, and the upper cover adjusted on the cylinder so that no space was left between it and the soil. The cylinder was then dug out carefully, so as not to disturb the soil it contained, the earth at the bottom smoothed off, and the lower cover tightly adjusted. It was then packed in cotton batting or similar shock insulating material to prevent disturbance of the soil while it was being carried to the laboratory.

The results obtained by Burger were felt to be sufficiently striking to warrant the use of the cylinder method in the present study. In the laboratory, the procedure employed by the writer was a slight modification of Wiegner's rapid method, used by Burger in part of his work. When the cylinders reached the laboratory, they were first weighed to determine the moisture content under field conditions. The top covers were then removed and the samples placed in a water bath of sufficient depth completely to cover them. In order to saturate the soil completely, they were allowed to remain in this bath for 24 hours. At the end of this time, each cylinder was covered under water, and then transferred, still under water, to a large open vessel. The cylinder was now suspended from one beam of a large balance, and weighed under water. To the weight thus obtained was added the previously determined weight of the volume of water displaced by the cylinder. The cylinder was then turned upside down, the bottom cover removed, and a triple thickness of cheesecloth placed over the soil and held in place by elastic bands. It was next righted, the top cover removed, and the cylinder set on a drain rack where it remained for one hour to remove gravitational water. At the end of this time the cylinder was again weighed. The difference between the result of this weighing and that of the fully saturated soil gave the weight of the gravitational water, hence the air space of the soil. The entire sample was then removed to a tared weighing pan and dried to a constant weight at 100° to 105°C. From the loss of weight upon drying was obtained the moisture content of the soil under optimum field conditions. The sum of the two water contents gave the total pore space of the soil. The difference between the pore space and the total volume of the cylinder gave the volume occupied by the soil. Hence the specific gravity and the volume weight could readily be calculated.

Burger (5) found the soils of the better forested areas notably more permeable to water than those either of the poorer forests or of pastures. He also noted that good forest land had the greatest air space, the most pore space, and the best water-holding capacity of any of the soils examined. With regard to these same factors, differences were found between several pasture types which appeared to correlate with the quality of the pastures. In the work carried on by the writer, it was at first attempted to use cylinders of

the size employed by Burger; that is, of 10 cm. in height and 100 sq. cm. in area. This was found extremely difficult to do, because of the large numbers of rocks encountered in the glacial soils of New York state. It was found, however, that in almost all instances it was possible to use a cylinder of smaller diameter than Burger's, and with heavier walls. The diameter of both cylinders (one used to determine water permeability, the other for volume weight, air space, etc.) was therefore reduced to 6.8 cm. These cylinders had a content of 363 cubic cm. The methods of manipulation were in all cases identical with those previously described.

The determination resulting from the use of the original Burger cylinders and from the modified cylinders are given in Table II. The most striking difference displayed in any of the physical factors is in the permeability of the soil to water. In the same area, there may be an appreciable variability in the time required for a head of 10 cm. of water to pass into the soil, but it is far less than the differences recorded between the good and the poor soils. In general, the forest soils were distinctly the more permeable, the time required for the water to enter them ranging, with one exception, from one-half minute to seven minutes. It was discovered that Sample No. 33, the exception just noted, came from a woods subject to occasional flooding in spring, a condition clearly reflected in the greater time required for the water to pass into this soil.

The blue grass soils were somewhat less permeable than the forest land. Here again one of the samples, No. 34, was from a pasture flat where water sometimes rose in the spring, and this soil was found to be more compact than were the other blue grass sods. The range of time on the normal blue grass soils was from two to ten minutes. This is a wide variation, but it will be seen that even the high figure is far below the time requirements in the compact soils. Though the best of the Rhode Island bent soils were as permeable as were the blue grass, the poorer soils of this group were decidedly less so. The sweet vernal soils had a range from 25 minutes to 45 minutes, which would cause them to be classed as moderately impermeable, while the poverty grass soils were the least permeable of all. Those supporting moss and fern were, like the sweet vernal group, moderately impermeable.

As for the other physical factors determined, the forest soils showed the best water holding capacity, and a slightly better air content than did any other set of the series. There were no distinctive differences between the better and the poorer groups, however, in any other of the factors tabulated. It is very probable that the variable content of rocks present in all these soils tend to obscure physical differences which may be inherent in the soil structure of the several pasture types.

Physical Analyses by Bouyoucos Hydrometer Method

In considering the soil profiles it was pointed out that there was a noticeably smaller root growth in the B horizons of the poorer pasture lands than was the case in the better pastures. There was also much less penetration of the roots into the lower subsoil, or C horizon. It therefore seemed desirable to discover whether this restricted root growth on the poorer pastures could be caused by a washing down of relatively impermeable colloidal material from the upper horizons into the lower subsoil. It was believed that such a change of colloidal content would have to be rather large to exert a marked influence upon root development.

To determine the possible change in colloidal content of the soil horizons, the Bouyoucos (1) hydrometer method was chosen. Several investigators, among them Gile (11) and Keen (15), have raised theoretical objections concerning the accuracy of the hydrometer method. In the present investigation it was found, however, that this procedure gave closely agreeing duplicate results upon the uniformly ground analytical samples passed through a 1 mm. sieve. A series of determinations made upon soils of varying textures, but of the same series as those embraced in the pasture types, showed that the method would indicate the physical differences between these soils. A measure of relative colloidal variation was believed to be of value, even though the results might not embody absolute accuracy.

The determinations of total sand, coarse silt, total colloids, total clay, and fine clay, by the hydrometer method, were made on the separate horizons of each profile. The procedure followed was exactly that outlined by Bouyoucos (1) in a recent publication.

The significant figures in the matter of the deposition of colloids in the lower soil horizons are the percentages of total colloids, total clay, and fine clay. Since the soils in each group are from several different series, and are also of slightly different physical texture, it would be inaccurate to determine the mean content of total colloids and total clay in the different samples of each horizon. A better measure of possible colloidal deposition would be the range of differences in colloidal content between the A, B, and C horizons in each soil. The detailed results will not be given here, but the important variations are shown in the following summary.

The extreme range of difference in colloidal and clay content between the A and the C horizons was determined for all the soils. There was an appreciable variability in this factor among each set of samples. In the forest soils, the increase in colloidal content of the C over the corresponding A horizon ranged from 2% up to 17%, with a mean of 7.76%. The blue grass samples were also variable, with an extreme range from 0 to 10.6%, and a mean of 3.6%. The Rhode Island bent soils ran from 0 up to 31%, with a mean of 9.27%; the sweet vernal from .7% to 11.9%, with a mean of

4.5% ; the poverty grass from 0 to 25%, with a mean of 7.4% ; and the moss and fern soils varied from 0 to 12% in colloidal content, with a mean difference of 6.2%. It is clear from these figures that there is no greater difference in colloidal content between the upper and lower horizons of the poor pastures than between those of the good pastures, or of the forest soils. In none of the groups under consideration, then, is there any evidence of unusual colloidal deposition, or of the washing down of colloids or clay from the upper to the lower horizons.

BACTERIOLOGICAL STUDIES

Nitrification and Ammonification

The nitrification and ammonification of the soil's own nitrogen was determined on each A sample after an incubation period of five weeks at room temperature, which ranged from 22° to 25°C. Fresh soil only was employed for this work. As soon as the samples were brought into the laboratory, a portion of each A sample was placed in a jar, which was then closed. These jars were kept in a refrigerator at a temperature of from 4.5° to 5°C. until the nitrifications were started. The usual tumbler method was used to determine the development of nitrate nitrogen and of replaceable ammonia nitrogen. The time of storage was five weeks, during which additions of water were made to maintain optimum moisture. The content of water-soluble nitrate nitrogen was determined in one portion of the soil at the commencement of the period of storage. In a separate portion, the initial content of replaceable ammonia was determined, essentially by the method of Harper (13).

At the close of the period of incubation, the samples were made up to their original moisture content. Half of each sample was then used for the determination of nitrate nitrogen. In the other half the replaceable ammonia was determined. At the start, the content of replaceable ammonia ranged from zero up to 12 parts per million of ammonia nitrogen. In the majority of the samples it ranged from 1 to 5 parts per million. At the close of the period of incubation, in over half the samples there was no replaceable ammonia. Only in one sample of any group was there an appreciable increase in replaceable ammonia. This sample, No. 30A, taken from a moss and fern pasture, contained 212 parts per million of ammonia nitrogen. The remainder of the samples contained essentially the same amount as at the beginning of the storage period. These determinations showed there was no great tendency for ammonia to accumulate in soils which possessed a low nitrifying power.

The results of the nitrification studies are given in Table III. Several striking facts are evinced by these determinations. At the start, the forest soils had in general the largest content of nitrates; they also made the largest consistent gains of nitrates after storage. The poorly aerated forest sample,

No. 33, displayed a relatively low content of nitrates at the beginning of the study, but made a large increase during the five weeks storage period. The Kentucky blue grass soils stood next to those of the forest in order of original nitrate content, and in increase in nitrates.

The Rhode Island bent soils showed considerable variation both in initial nitrates and in the gains made during storage. In most instances, the best gains in this group were made by the soils from the best pastures. All the poverty grass soils were extremely low in their original nitrate content; the gains they made varied decidedly. One of the largely organic A horizon soils, No. 17A, showed a large gain, but the indication is that the nitrogen of this accumulated organic matter is not readily available. Sample No. 16A, which also showed a large amount of organic matter, gave only a moderate gain, while in No. 18A, another highly organic sample, there was no increase.

The moss and fern soils, like those from the poverty grass pastures, all showed a small initial supply of nitrates, and the gains made by most of them were very poor. Although one sample, No. $30A_1$, made a large increase, it was representative of an A horizon only 3 cm. in thickness, and the sample from the underlying A_2 horizon showed a relatively small gain in nitrates.

In general, the results of the nitrification studies indicate that a good content of nitrates and a high nitrifying power are associated with the better pasture and forest soils. The results of the experiments are presented graphically in Figure 1.

Determination of Presence of Azotobacter Chrococcum

All the A horizon samples were examined for the presence or absence of nitrogen fixing bacteria, *Azotobacter chrococcum*. The first of the two methods employed in making these determinations was Winogradsky's (27) molded plate culture method. In accordance with this procedure, four portions of the soil to be examined were treated with mannite at the rate of 1 gram per 100 grams of soil. In addition, one portion of the four received Ca CO_3 at the rate of 2 or 3 grams per hundred; a second was moistened with potassium or sodium hydrogen phosphate of a strength of 1 gram to 1,000 cc.; a third was treated with both lime and phosphate solution. The portion treated with mannite alone, as well as the one to which Ca CO_3 was added, was moistened with distilled water. The smoothly mixed, pasty soils were transferred to petrie dishes and struck off smoothly across the top. They were then incubated in a moist chamber for a period of forty-eight hours, at a temperature of 30°C. At the end of this time they were examined, and the Azotobacter colonies were noted as clear, viscous masses on the surface of the smooth soil. Where these colonies were present, an increased growth on the plates treated with lime and phosphate was considered to indicate a deficiency of these materials in the original soil.

The results obtained from the spontaneous plate culture method were of course qualitative, and they were supplemented by a quantitative investigation, in which the numbers of Azotobacter were determined by inoculating tubes of Ashby's medium with diluted soil suspension.

The results of the examination of all soil samples from the A horizons indicated that the presence or absence of Azotobacter is a minor factor in any of the groups of soils included in this investigation. Only two samples from Kentucky blue grass pastures, Nos. 4 and 6, were found to have Azotobacter present; both of them had a numerous Azotobacter population. The pastures from which these samples were taken were among the best included in this study, but the absence of Azotobacter from the balance of the areas of all types, many of which were quite fertile, indicates that Azotobacter activity is not an important factor in maintaining the nitrogen supply of the forest and pasture lands under discussion.

Presence of Legume Organisms

In the review of the literature covering the fertilization of pasture lands, it was frequently noted that one of the most favorable results produced by fertilizer treatments was an increase in the percentage of legumes present in the herbage. A soil condition favorable for the growth of legumes frequently brought clovers into pastures where they had not before been present, and where no legume seed had been planted. An improvement of this sort would depend upon legume inoculating organisms, such as *Bacillus radicicola*, occurring in the soil. It seemed to be desirable, therefore, to discover whether legume bacteria were generally present in the pastures under observation.

The method employed was to plant tumblers of sterile soil with chemically sterilized legume seed, and then to inoculate them with quantitative dilutions of the fresh pasture soils. By this procedure it was possible to determine both the presence and numbers of legume organisms occurring in the various soils of the pasture groups. It was found that few of the forest soils possessed legume bacteria, and that in only one sample, No. 33A, were they present in large numbers. Two of the Kentucky blue grass pastures, Nos. 3 and 34, had legume organisms present in the soil, and a reference to field notes showed that in these two pastures clover had been growing among the forage plants. Legume bacteria appeared in four of the Rhode Island bent samples, in two of the poverty grass pastures which were growing on run down Ontario loam, and appeared in considerable numbers in four of the moss and fern samples.

From these results it appears evident that legume bacteria are not generally present in these pasture soils, unless legume plants have recently been growing upon them.

Chemical Determinations Upon Forest and Pasture Soils

Soil Reaction and Chemical Composition

The results of the determination of the soil reaction, total nitrogen, organic carbon, total calcium, total magnesium, and total phosphoric acid are given in Table IV. In order that the reader may judge as to the relative portions of the profile occupied by the principal horizons, the depths in centimeters of the A_1, A_2, and B horizons is included in this table. The soil reaction was in all cases determined upon the fresh profile samples as soon as they reached the laboratory. All other determinations were made upon dried and ground samples. The preparation of the samples and the analyses upon them were carried out according to the methods of the Association of Official Agricultural Chemists (1925).

Soil Reaction. The mean value of the reaction of each portion of the profiles in the group of soils, as well as the probable error or the mean, has been computed and is included in Table IV. The values show all portions of the profiles of the Kentucky blue grass soils to have been either neutral, or slightly alkaline. The forest and Rhode Island bent soils had a slightly acid reaction, ranging around a pH of 6.0. The sweet vernal, poverty grass, and moss and fern soils all showed increasing degrees of acidity. The poverty grass soils included in this tabulation are those from the four areas where poverty grass alone predominated.

Total Nitrogen. No very accurate deductions can be made from the figures for total nitrogen because of the previously discussed accumulation of undecomposed plant residues in the A_1 horizons of some of the poorer soils. Also, it was found extremely difficult to free the soils from particles of grass and plant roots. The nitrification of the fresh soils, which had as far as possible been freed from roots, is believed to give a truer picture of the availability of the nitrogen than does the total nitrogen determined on the dried samples. The nitrogen figures do show, however, the relatively large content of nitrogen in the thin A_1 horizons of several of the poorer pastures. But the nitrification studies have already demonstrated this nitrogen to be decidedly unavailable.

Total Organic Carbon. The total organic carbon was determined by the moist combustion method, as given in the official procedure. The accumulation of undecomposed plant residues in the A_1 horizons of some of the poorer pastures has previously been discussed in some detail, and it has also been pointed out that the nitrification studies showed a low availability of nitrogen in most of these organic materials. This made it desirable to discover if the low availability of nitrogen as well as the failure to decompose dead plant tissue, might not be associated with a poor oxidizing power of the soil. Schreiner and Sullivan (20) some years ago showed that the development of the red oxidized color of an aloin solution was a good measure of the oxidiz-

ing power of the soil. A series of selected samples were accordingly taken from the soils which had either very good, or very poor, nitrifying power. A number of these were also high in their percentage of organic carbon. The results of the oxidization of aloin are given in Table V. The soils which were high in nitrates showed, in general, a strong development of the red oxidized color of aloin. It appears probable that the low development of nitrates in many of the pasture samples is associated with a low oxidizing power in these especial soils.

The carbon nitrogen ratio has been calculated for all of the samples and is included in Table IV. On the great majority of the samples, the ratio is considerably wider than the ratio of 1 : 10 which has been found on cultivated soils. The forest soils showed an appreciable variability in the carbon nitrogen ratio; the mean value for the A horizon was 16.1, for the A_2 8.9, for the B 19.1, and for the C, 15.1. The values obtained on the blue grass samples were more consistent; they were 14.5, 14.2, 15.1, and 16.8 for the successive portions of the profile. Approximately these same figures were found for both the Rhode Island bent and sweet vernal samples. The mean values for poverty grass and the moss and fern soils in most cases showed a wider ratio than did those of any of the other groups.

Total Calcium. The figures for total calcium show that there is a significant difference in the amount of this material present in the good and the poor soils. This relationship is brought out clearly in Figure 3, which represents the mean calcium percentage of the horizons of each of the six groups of soils. The surface horizons of the Kentucky blue grass pastures have the highest content of calcium; the forest and the Rhode Island bent soils a slightly lower one. The notable difference, however, is between the calcium found in the three groups of better soils, and that occurring in the sweet vernal, the poverty grass, and the moss and fern pastures. The percentage of calcium present in the four typical poverty grass soils was calculated separately from the mean content of all the samples of this group. The graphic representation of these figures makes clear the steady decrease in calcium from surface horizon to lower subsoil.

Total Magnesium. The mean percentage of total magnesium in the forest and the pasture soils is shown in Figure 4. It will be seen that the blue grass pastures have a consistently higher magnesium content than that occurring in any other group. The amount of magnesium present in each of the remaining five sets of soils is not conspicuously different, except that the moss and fern soils show rather a low percentage of magnesium in their surface horizons.

Total Phosphorus. The mean values for total phosphorus are graphically represented in Figure 5. The Kentucky blue grass soils contain more phosphorus in the surface horizons than is present in those of any of the other

sets, but the difference is not so great as was the case either with calcium or magnesium. Beyond this slightly higher level in the blue grass pastures, one cannot discover in the phosphorus content differences sufficiently great to be significant.

Available Phosphates and Calcium. The attempt to determine the available nutrients in soils has resulted in the development of a large number of methods. Perhaps there are none of them which can be regarded as entirely satisfactory for all conditions. In the present investigation, two procedures were employed in an attempt to obtain some indication of the availability of phosphates, lime, and potash. The content of available phosphates was determined in all the samples by the "Illinois Rapid Test." The procedure followed was essentially that developed by Bray (2). Only two modifications were introduced: the mixture of soil and reagent was filtered in order to remove suspended material and the molybdenum blue color was developed by the addition of a minute crystal of stannous chloride.

The results of the examinations of all the profile samples are given in Table VI. It will be seen that a greater number of the A horizon samples of forest soils showed a high content of available phosphate than did those of any other group. There were a larger number of high phosphate tests in the blue grass samples than in the other pasture samples. The sweet vernal soils, those of the typical poverty grass areas, and the moss and fern soils gave indications of lower available phosphates than was the case in those of the better pasture types.

The second procedure used to determine the availability of calcium, phosphates, and potash was a modification of Winogradsky's molded plate culture method. Through the courtesy of Dr. J. K. Wilson, the writer was supplied with a pure culture of *Azotobacter chrococcum.* This culture was used to inoculate six portions of each soil horizon sample. One portion was then treated with mannite alone, a second with sodium phosphate, a third with potassium phosphate, a fourth with calcium carbonate, a fifth with calcium carbonate plus sodium phosphate, and the sixth with calcium carbonate and potassium phosphate. The detailed results of these tests will not be given here, since it was found that all the samples of the A and the B horizons gave some degree of response to calcium. Since the method is qualitative, small variations cannot readily be recorded. In nearly every case there was, in addition, some increased growth when phosphates were added. The subsoil samples with a high content of lime showed no increase upon the addition of calcium, but did display some additional growth of Azotobacter where phosphates had been added. There was no consistent evidence of a response in Azotobacter growth to the addition of potassium phosphate to the soil, over that obtained where sodium phosphate was used.

The results obtained from the Azotobacter availability test do not conflict

with those from the Illinois Rapid Test. And they show an especial agreement with the results of most of the pasture fertilization studies in the northeastern states, these having shown a fairly general response to lime and phosphate fertilization.

DISCUSSION

A careful survey of the literature dealing with pasture investigations, both in the United States and abroad, has been made; but here only a brief summary will be given of such conclusions as bear upon the pasture problems of the Northeastern United States. In this section, extending from Virginia to Massachusetts, the finest pastures are those which possess Kentucky blue grass, or blue grass and clover sods. Throughout this area, many of the pastures which formerly supported Kentucky blue grass have deteriorated, and the original desirable grass has been replaced by inferior species and by weeds. Where moisture has been abundant, it has often been supplanted by Rhode Island bent. Under less favorable conditions it has been crowded out by poorer grasses, such as sweet vernal and poverty grass. Only under the most favorable conditions can Kentucky blue grass itself be indefinitely maintained as the dominant cover, without the aid of lime or fertilizer treatment.

Experiments in West Virginia (6), Pennsylvania (23 and 24), and Connecticut (3) have clearly shown that Kentucky blue grass can be restored on run-down pastures, if the fertility of the soil is improved. In most cases, the best response in grass growth has been obtained from the application of both lime and phosphates. Manure has given an excellent increase, where it has been available. In the experiments in Pennsylvania and Connecticut, gains in the forage crop were also reported as the result of the application of potash. Pasture studies conducted in Massachusetts (14) have indicated that potash was more effective than either acid phosphate or ground limestone, used alone. This result is unusual, and it would appear probable that the experiment was conducted on a soil which had a notable deficiency in available potash.

In the New York State experiments carried on by Wiggans (26) on a very poor soil, little response was obtained from potash fertilization. Excellent returns, on the other hand, resulted from the application of lime and phosphate. Conflicting reports have been made upon the effect of nitrogenous fertilization. The earlier studies indicated that nitrogen resulted in a large development of grass. Now it is claimed that where nitrogen is applied in combination with lime, potash, and phosphates, in accordance with the Hohenheim system (17), the growth of legumes has been greatly stimulated.

There is rather general agreement that cultivation or harrowing of pastures not only fails to benefit them, but may actually work them an injury. Reseeding of Kentucky blue grass or clovers has not been found necessary, if even a few plants of these species survive in a run down pasture. The

restoration of the fertility of the soil appears to be the essential condition for enabling blue grass and clovers to re-establish themselves on pasture land.

In the light of the foregoing conclusions, drawn from experiments carried out in several states, the results of the present investigation may now be considered. In the studies included in this piece of work, it has been attempted to determine the state of fertility of four important pasture types. Comparisons have been drawn between these pastures and a group of fertile forest areas, as well as with a series of typical moss and fern lands. It is believed that the evidence assembled enables one to judge of the change in physical state and fertility that accompanies the transition from forest cover to pasture grass types of decreasing value.

The work on soil profiles has shown that the original hardwood forest soils were in a better physical state than are any of the resulting pastures. The change from trees to grass resulted in a loss of permeability to water, a lower water holding capacity, and a loss of air space. The forest soils had a visibly better crumb structure of the earth-worm mull type than any of the pastures. The fertile Kentucky blue grass land most nearly approached the forest mull in texture. The forest soils and the better pasture types had significantly deeper A and B horizons than did the poor grazing land, or the moss and fern areas. This was shown in the depth of color of their disintegrated organic matter, as well as in the higher content of carbon in the forest soils. The root growth of Kentucky blue grass and Rhode Island bent was more extensive than that of the poorer grasses. Their roots occupied a greater proportion of the upper horizons of the soil and showed some tendency to penetrate into the lower, or C. horizon. The sweet vernal, poverty grass, and moss and fern plants were inclined to form a thick mat of roots at the surface of the ground. In many of the poor pastures this matted growth of roots was associated with the accumulation of undecomposed plant residues in a layer from 1 to 3 cm. in thickness. The organic matter contained in this layer was found to be relatively unavailable, hence there was, under these conditions, an actual locking up of part of the potential fertility of the soil.

Physical analyses of the soils by the hydrometer method has shown that there has been no abnormal washing down of soil colloids into the lower horizons of the poorer pastures. The differences in colloidal percentages between the surface soils and subsoils of the poorer areas were no greater than were those between the corresponding horizons of the productive pastures, or of the forest soils. The results of these physical studies warrant us in concluding that the change from hardwood forest cover even to the best of pasture forage results in some deterioration in the physical state of the soil. And this deterioration becomes, of course, more appreciable in the poorer pasture types.

The determination of the nitrifying power of the soil showed the forest

soils to possess the highest initial content of nitrates. Such soils also made the highest gains in nitrate production after storage. Next best in nitrate supply and development stood the Kentucky blue grass soils, while the Rhode Island bent soils ranked third. The soil from the poor pastures had a uniformly low nitrate content when collected, and in general made poor nitrate gains during storage. In most cases, the nitrogen of the organic matter of the poor areas was found to be slowly available. The activity of nitrogen fixing bacteria was found to be a minor factor, both in the good and the poor land. An appreciable number of Azotobacter were present in only two of the blue grass pastures, and in all other areas these organisms were lacking. Legume nodule bacteria occurred in part of the pasture and forest soils. In general, they were discovered only in those soils upon which legumes were growing. This indicates that in most cases soil inoculation would be necessary for the successful development of a legume flora.

The chemical analyses have shown a number of striking differences between the soils of the better and the poorer types. The Kentucky blue grass soils were distinctly the best of any of the pasture associations. This was shown by their possessing: a soil reaction close to neutrality, the highest lime content of any of the groups, the highest magnesium percentage, and the highest supply of phosphates.

The results of the analyses of total nitrogen and total carbon, if interpreted in the light of the nitrification studies, would indicate the forest soils to have possessed the largest supply of available carbon and nitrogen of any group. In this respect they were clearly superior to the blue grass pastures. From the results of the Illinois Rapid Test there was indication that the forest soils also possessed the largest amount of available phosphates.

From these determinations the deduction may be drawn that the hard wood forest soils used as a standard of comparison were not only in the best physical state of any of the groups of soils, but that they also had the largest amount of available nitrogen and carbon, and possibly the best content of available phosphates. The high level of mineral nutrients present in the Kentucky blue grass soils suggests that the land supporting this grass may originally have been even more fertile than the forest areas included in this study. A reference to the graphic comparisons of the mean content of total calcium, total magnesium, and total phosphates, given in Figures 3, 4, and 5, will make evident the similarity of the content of nutrients in the forest soils to that of the Rhode Island bent, and the superiority of that of the blue grass soils to either of the others. If the forest soils were to be deprived of their excellent physical texture, and of their excess available nitrogen and carbon, they would be more comparable to the Rhode Island bent soils than to the typical blue grass land.

The Kentucky blue grass pastures sampled are known to have supported

this grass for many years. It is therefore the belief of the writer that the condition of high fertility found in these soils is a state necessary for the successful growth of Kentucky blue grass. The results obtained will be seen to agree with those of the other pasture experiments carried out in the northeastern states.

In conclusion it may be suggested, on the basis of the work carried out here in New York State and in adjoining states, that the poorer pasture types, such as those so designated in this investigation, can in many cases be restored to a state of fertility. The application of lime and superphosphate is likely to bring about the greatest improvement in grass and in leguminous growth. The addition of manure will cause an immediate gain in the forage crop. Although in New York State the use of potash has not resulted in large returns in pasture growth, in any system of pasture renovation it should be applied experimentally to part of the area. The favorable results so far reported from tests of the Hohenheim system would warrant some intensive studies of pasture improvement; using this system of nitrogen application in combination with lime, phosphates, and potash.

SUMMARY

(1) The typical soil conditions associated with the growth of hardwood forest, Kentucky blue grass, Rhode Island bent, sweet vernal, and poverty grass pastures, and moss and fern land have been investigated.

(2) The forest soils have been used as a measure of the fertility which may have been present in the pasture land when it was covered with trees.

(3) Each soil profile was excavated and mapped from the A to the C horizon.

(4) The change from trees to grass has resulted in a loss of permeability to water, a smaller water holding capacity, and lessened air space.

(5) The forest soils and the Kentucky blue grass and Rhode Island bent pastures have deeper, more humified A and B horizons than have the poor pastures or the moss and fern lands.

(6) The root growth of Kentucky blue grass and Rhode Island bent has been uniformly deeper than that of the poorer grasses.

(7) The sweet vernal, poverty grass, and moss and fern plants have tended to form a thick mat of roots at the surface of the soil.

(8) In many poor pastures, plant residues have accumulated in a compact mat, 1 to 3 cm. deep, which formed the A_1 horizon of the soil. These plant residues decompose slowly, so that grass is choked out.

(9) Physical analyses of the soils were made by the hydrometer method. These analyses showed that there has been no abnormal washing down of colloidal materials into the lower horizons of any of the soils.

(10) The forest soils had the highest initial content of nitrates of any of the groups, and developed the largest amounts of nitrates during storage.

(11) The Kentucky blue grass soils ranked next to the forest soils in nitrate activity, and were followed by the Rhode Island bent soils. The poor soils showed small amounts of nitrates present at the time of sampling, and in general made poor gains during incubation.

(12) Azotobacter was present in only two soils, and those were from the Kentucky blue grass group.

(13) Legume bacteria were found only in the soils on which legumes had been growing. Many pastures will require inoculation before legumes will develop.

(14) The Kentucky blue grass pastures sampled were located on Ontario loam soils, or on similar high lime soil series. All portions of their profile were more nearly neutral than were the forest soils or the Rhode Island bent pastures. In most instances, the poor land was more acid in reaction. The run down pastures on neutral soil have been heavily invaded by weeds, rather than by inferior grasses.

(15) The forest soils had an appreciably larger content of total nitrogen and total carbon than the pastures on the same soil series. The poor pastures had, in many cases, a considerable content of unavailable nitrogen and carbon from undecomposed plant residues.

(16) The results of the investigation indicate that Kentucky blue grass is the normal pasture cover for high lime soils that are well supplied with nutrients, the Rhode Island bent is likely to occur on pastures located upon soils of lower lime content and moderately acid reaction.

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TABLE I. *Classification of forest and pasture areas and predominating forest cover.*

Sample No.	Description of Area	Type of Growth	Soil Classification	General Location of Sample	Adjacent Forest
4.......	Hardwood Forest Soil	Excellent	Palmyra Gravelly Loam	Oneida County	Maple, Beech, Chestnut
8.......	"	"	Ontario Loam	Chenango County	Maple, Beech, Oak, Hickory
11.......	"	"	Wooster Loam	Chenango County	Maple, Beech, Hickory
20.......	"	"	Ontario Loam	Onondaga County	Maple, Beech, Basswood
21.......	"	"	Ontario Loam	Onondaga County	Maple, Beech, Basswood
33.......	"	"	Wooster Gravelly Silt Loam	Tompkins County	Maple, Oak, Hickory, Basswood
1.......	Kentucky Bluegrass Pasture	Excellent	Ontario Loam	Ontario County	Maple, Oak, Hickory
2.......	"	"	Ontario Loam	Ontario County	Maple, Oak, Hickory
3.......	"	"	Palmyra Gravelly Loam	Oneida County	Maple, Beech, Elm, Ash
5.......	"	"	Ontario Loam	Oneida County	Maple, Elm, Ash
6.......	"	"	Ontario Laom	Chenango County	Maple, Beech, Oak, Hickory
34.......	"	"	Genesee Loam	Cayuga County	Maple, Elm, Ash
13.......	Rhode Island bent pasture	Good	Chenango Gravelly Loam	Chenango County	Maple, Beech, Pine, Hemlock
14.......	"	Poor Sod	Wooster Gravelly Loam	Chenango County	Maple, Beech, Pine
15.......	"	Fair	Wooster Gravelly Loam	Chenango County	Maple, Beech, Elm
19.......	"	Very Good	Ontario Loam	Cortland County	Maple, Beech, Hickory
24.......	"	Good	Farmington Silt Loam	Herkimer County	Beech, Maple, Birch, Elm
25.......	"	Fair	Hinckley Fine Sandy Loam	Herkimer County	Maple, Beech, Hemlock
26.......	"	Good	Farmington Silt Loam	Herkimer County	Beech, Elm, Maple
7.......	Sweet vernal pasture	Poor	Volusia Silt Loam	Chenango County	Maple, Pine, Hemlock
9.......	"	Poor	Wooster Silt Loam	Chenango County	Maple, Beech, Pine, Hemlock
12.......	"	Fair	Chenango Gravelly Loam	Chenango County	Maple, Beech, Pine, Hemlock
10.......	Poverty grass pasture	Poor	Wooster Silt Loam	Chenango County	Maple, Beech, Pine, Hemlock
16.......	"	Poor	Wooster Gravelly Silt Loam	Chenango County	Maple, Beech, Hemlock
17.......	"	Poor	Volusia Gravelly Silt Loam	Chenango County	Maple, Beech, Elm
18.......	"	Poor	Wooster Gravelly Silt Loam	Chenango County	Maple, Beech, Hemlock
22.......	Poverty grass in Canada bluegrass	Fair	Ontario Loam	Onondaga County	Maple, Beech, Elm

Table I. *(Continued)*

Sample No.	Description of Area	Type of Growth	Soil Classification	General Location of Sample	Adjacent Forest
23.......	Poverty grass and weeds	Poor	Ontario Sandy Loam	Onondaga County	Maple, Aspen, Hemlock, Elm
27.......	Moss and fern pasture	Poor	Culver Sandy Loam	Delaware County	Maple, Pine, Hemlock
28.......	"	"	Culver Sandy Loam	Delaware County	Maple, Beech, Elm
29.......	"	"	Walton Sandy Loam	Delaware County	Maple, Beech, Hemlock
30.......	"	"	Walton Sandy Loam	Delaware County	Beech, Maple, Pine
31.......	"	"	Hamden Sandy Loam	Delaware County	Maple, Elm, Hemlock
32.......	"	"	Culver Stony Silt Loam	Delaware County	Maple, Beech, Pine

TABLE II. *Physical factors determined on forest and pasture soils by cylinder methods of Burger*

Sample No.	Description of Area	Specific Gravity	Volume Weight	Maximum Moisture Capacity	Moisture Content in field	Total Pore Space	Air Content at Maximum Capacity	Permeability to 10c.m. Water Mins.
4A....	Forest plot	....	....	....	....	....	....	4.6
8A....	" "	2.22	.861	64.02	41.37	62.71	7.76	5.5
11A....	" "	2.30	.528	126.33	55.15	77.68	19.23	4.0
20A....	" "	2.41	1.064	45.67	32.33	50.75	7.15	3.5
21A....	" "	3.26	.569	90.82	56.00	82.57	31.16	1.3
33A....	" "	2.80	.988	50.84	29.7	64.79	14.56	27.0
1A....	Kentucky blue grass pasture	2.13	.874	61.51	29.84	59.06	5.27	7.2
2A....	" "	2.19	.964	53.77	32.33	55.93	4.05	3.5
3A....	" "	.....	.....	.....	.....	.....	.....	8.0
5A....	" "	2.34	1.177	39.38	25.95	49.67	3.35	9.0
6A....	" "	2.61	.857	61.60	30.80	53.86	14.35	2.5
34A....	" "	2.65	1.224	38.82	17.57	53.93	6.41	59.0
13A....	Rhode Island bent pasture	2.64	.973	52.82	15.36	63.15	11.87	6.6
14A....	" "	2.62	1.029	52.61	40.80	60.79	6.61	78.0
15A....	" "	2.95	.959	70.47	32.13	67.55	16.05	3.2
19A....	" "	2.71	.997	51.40	30.15	62.92	11.66	2.2
24A....	" "	2.73	.971	59.54	43.04	64.42	6.76	52.3
25A....	" "	2.60	1.043	50.51	20.11	59.96	7.26	55.0
26A....	" "	2.78	1.002	55.84	31.61	63.93	7.97	85.0
7A....	Sweet vernal pasture	2.31	1.038	49.81	31.98	55.10	3.40	44.0
9A....	" "	2.52	.880	63.70	22.73	65.06	9.32	26.0
12A....	" "	2.48	.817	74.44	31.14	66.55	5.70	41.0
10A....	Poverty grass pasture	2.71	1.087	46.56	24.02	59.96	9.89	24.
16A....	" "	2.62	.929	61.60	43.12	64.54	7.38	70.
17A....	" "	2.80	.969	55.23	35.77	65.35	11.80	29.0
18A....	" "	.....	.....	.....	.....	.....	.....	51.0
22A....	" "	2.81	1.241	34.22	23.88	55.84	13.36	48.0
23A....	" "	3.30	1.066	52.11	33.09	67.12	11.94	26.0
27A....	Moss and fern pasture	2.90	.957	56.67	26.02	66.98	12.87	35.0
28A....	" "	2.77	.835	69.19	22.76	69.24	11.94	26.0
29A....	" "	2.72	.969	54.76	22.05	64.35	11.37	13.5
31A....	" "	2.79	1.226	40.14	15.13	55.98	6.83	56.5

TABLE III. *Results of nitrification of pasture and forest soils. Period of incubation was five weeks in all cases.*

Sample No.	Description	Soil Reaction pH	Nitrate Content at Start ppm NO_3	Nitrate Content of Duplicates at Close ppm NO_3	Average Nitrate Content at Close ppm NO_3	Gain in Nitrates ppm No_3
4A....	Forest soil	6.50	47.6	258.2 258.2	258.2	210.6
8A....	" "	6.52	26.7	103.4 107.8	105.6	78.9
11A....	" "	5.22	66.1	465.7 465.7	465.7	399.6
20A....	" "	6.49	79.2	201.1 214.0	207.5	128.3
21A....	" "	6.41	129.4	358.0 358.0	358.0	228.6
33A....	" "	5.75	6.9	73.2 73.2	73.2	66.3
1A....	Blue grass pasture	7.68	28.9	188.4 191.6	190.0	161.1
2A....	" "	7.42	18.9	63.9 60.8	62.3	43.4
3A....	" "	6.47	10.0	57.7 56.9	57.3	47.3
5A....	" "	7.92	27.8	83.1 89.4	86.2	58.4
6A....	" "	6.67	136.0	571.2 527.9	549.5	413.5
34A....	" "	7.60	11.9	93.7 93.7	93.7	81.8
13A....	Rhode Island bent pasture	5.96	3.7	59.1 59.1	59.1	55.4
14A....	" "	5.37	1.5	3.4 4.4	3.9	2.4
15A....	" "	5.60	2.2	23.9 25.7	24.8	22.6
19A....	" "	5.80	29.4	164.8 167.0	165.9	136.5
24A....	" "	6.61	32.9	70.6 74.5	72.5	39.6
25A....	" "	5.89	11.5	64.2 64.2	64.2	52.7
26A....	" "	5.97	5.3	4.1 4.1	4.1	-1.2
7A....	Sweet vernal pasture	5.67	3.3	11.7 8.3	10.0	6.7
9A....	" "	5.77	8.0	61.5 70.4	65.9	57.9
12A....	" "	5.65	2.9	43.1 43.1	43.1	40.2
10A....	Poverty grass pasture	5.76	1.8	8.5 5.3	6.9	5.1
$16A_1$....	" "	4.82	2.7	44.5 37.4	40.9	38.2
$16A_2$....	" "	5.18	1.3	19.5 26.3	22.9	21.6
$17A_1$....	" "	5.18	5.7	191.3 191.3	191.3	185.6
$17A_2$....	" "	5.57	1.5	8.7 6.7	7.7	6.2

TABLE III. *(Continued)*

Sample No.	Description	Soil Reaction pH	Nitrate Content at Start ppm NO_3	Nitrate Content of Duplicates at Close ppm NO_3	Average Nitrate Content at Close ppm NO_3	Gain in Nitrates ppm NO_3
18A....	Poverty grass pasture	5.05	3.8	3.1 3.1	3.1	-0.7
22A....	" "	7.50	7.5	71.9 70.6	71.2	63.7
23A....	" "	7.92	4.6	47.1 39.4	43.2	38.6
27A....	Moss and fern pasture	4.74	4.2	3.0 3.0	3.0	-1.2
$28A_1$...	" "	5.12	9.2	10.5 10.5	10.5	1.3
$28A_2$...	" "	5.15	8.8	15.8 14.9	15.3	6.5
29A....	" "	4.85	11.9	31.2 31.7	31.5	19.6
$30A_1$...	" "	5.75	11.2	332.4 354.0	343.2	332.0
$30A_2$...	" "	5.37	6.0	35.5 35.5	35.5	29.5
31A....	" "	5.06	5.6	27.0 21.8	24.4	18.8
32A....	" "	5.20	7.5	11.1 11.8	11.4	3.9

TABLE IV. *Chemical composition of forest and pasture soils. Results calculated to the water-free basis.*

Sample No. and Horizon	Description	Depth of Horizon Centimeters	Soil Reaction pH	Total Nitrogen N%	Organic Carbon C%	Ratio Carbon Nitrogen	Total Calcium CaO %	Total Magnesium MgO %	Total Phosphorus P_2O_5%
4A1	Forest soil	3.0	6.50	0.634	10.77	17.0	1.22	0.96	0.239
4A2	" "	7.5	5.82	0.641	5.04	7.9	0.78	0.85	0.197
4B	" "	20.0	5.97	0.269	4.10	15.2	0.76	0.89	0.149
8A	" "	21.0	6.52	0.378	6.35	16.8	1.30	1.21	0.098
8B	" "	59.0	6.44	0.051	1.64	32.1	2.52	1.38	0.109
8C	" "	....	8.35	0.065	0.84	12.9	0.48	1.01	0.096
11A	" "	13.0	5.22	0.518	7.64	14.7	0.65	0.81	0.247
11B	" "	15.0	4.86	0.253	3.16	12.5	0.37	0.77	0.201
11C	" "	....	4.72	0.128	1.54	12.0	0.96	0.79	0.172
20A	" "	15.0	6.49	0.316	5.26	16.6	1.28	0.18	0.168
20B	" "	25.0	5.49	0.134	2.14	16.0	0.77	0.30	0.126
20C	" "	....	5.75	0.042	0.76	18.1	0.84	0.31	0.094
$21A_1$	" "	8.0	6.41	0.340	5.62	16.5	1.48	0.40	0.210
$21A_2$	" "	6.0	6.14	0.220	2.21	10.0	1.14	0.33	0.180
21B	" "	30.0	5.39	0.103	2.18	21.2	0.84	0.50	0.135
33A	" "	14.0	5.75	0.286	4.24	14.8	1.08	0.58	0.199
33B	" "	18.0	5.60	0.099	1.74	17.6	0.65	0.52	0.111
33C	" "	....	6.03	0.048	0.69	14.4	0.67	0.55	0.114
Mean A_1	" "	....	6.15 ± 0.14	$0.412 \pm .034$	0.65 ± 0.58	16.1	1.16 ± 0.07	0.69 ± 0.03	0.193 ± 0.014
Mean A_2	" "	....	5.98 ± 0.06	$0.430 \pm .105$	3.62 ± 0.55	8.9	0.96 ± 0.06	0.59 ± 0.10	0.188 ± 0.004
Mean B	" "	....	5.62 ± 0.14	$0.151 \pm .022$	2.49 ± 0.24	19.1	0.99 ± 0.20	0.72 ± 0.09	0.138 ± 0.008
Mean C	" "	....	5.89 ± 0.37	$0.069 \pm .0008$	0.93 ± 0.09	15.1	0.76 ± 0.05	0.65 ± 0.07	0.101 ± 0.009
1A	Blue grass pasture soil	14.0	7.68	0.374	5.45	14.6	2.03	1.12	0.190
1B	" "	20.0	7.85	0.089	1.44	16.2	1.62	1.18	0.113
1C	" "	....	8.22	0.082	1.51	18.4	1.59	1.56	0.163
2A	" "	18.0	7.42	0.258	4.45	17.3	1.52	0.89	0.139
2B	" "	35.0	7.12	0.070	1.37	19.6	1.32	0.75	0.090
3A	" "	10.0	6.47	0.202	3.49	17.3	1.81	0.82	0.212
3B	" "	20.0	6.57	0.133	2.04	15.3	0.78	1.19	0.232
3C	" "	....	7.22	0.069	1.46	21.2	0.74	1.01	0.108
$5A_1$	" "	11.0	7.92	0.279	3.83	13.7	1.86	2.69	0.208
$5A_2$	" "	8.0	7.92	0.142	2.23	15.7	2.08	3.02	0.190

TABLE IV. *(Continued)*

Sample No. and Horizon	Description	Depth of Horizon Centimeters	Soil Reaction pH	Total Nitrogen N%	Organic Carbon C%	Ratio Carbon Nitrogen	Total Calcium CaO %	Total Magnesium MgO %	Total Phosphorus P_2O_5%
5B......	Blue grass pasture soil	45.0	7.97	0.049	0.62	12.7	0.63	2.77	0.113
5C......	" "	....	7.60	0.042	0.46	11.0	0.63	1.72	0.084
6A1.....	" "	11.0	6.67	0.652	7.78	11.9	1.09	0.76	0.502
6A2.....	" "	18.0	6.32	0.330	4.19	12.7	0.52	0.83	0.260
6B......	" "	41.0	5.40	0.125	1.92	15.4	0.69	0.86	0.262
34A......	" "	18.0	7.60	0.375	4.53	12.1	0.78	0.52	0.211
34B......	" "	20.0	7.10	0.272	3.05	11.2	0.77	0.55	0.222
Mean A1.	" "	....	7.29±.15	0.356±0.04	4.92±0.39	14.5	1.51±0.12	1.13±0.20	0.244±0.025
Mean A2.	" "	....	7.12±.38	0.236±0.04	3.21±0.27	14.2	1.29±0.38	1.92±0.52	0.225±0.017
Mean B..	" "	....	7.00±24	0.123±0.02	1.74±0.20	15.1	0.97±0.05	1.21±0.20	0.172±0.018
Mean C..	" "	....	7.68±16	0.064±0.006	1.14±0.19	16.8	0.98±0.13	1.43±0.12	0.118±0.013
13A......	Rhode Island pasture soil	13.0	5.96	0.324	5.41	16.7	0.95	0.70	0.171
13B......	" "	20.0	5.56	0.183	3.03	16.6	0.56	0.73	0.139
13C......	" "	....	4.95	0.135	2.71	20.1	0.75	0.51	0.085
14A......	" "	15.0	5.37	0.273	5.36	19.6	0.50	0.27	0.140
14B......	" "	15.0	5.39	0.183	2.70	14.8	0.30	0.72	0.129
14C......	" "	....	5.54	0.065	1.03	15.8	0.72	0.71	0.112
15A......	" "	29.0	5.60	0.330	4.71	14.3	1.05	0.62	0.197
15B......	" "	31.0	5.78	0.203	2.81	13.8	0.88	0.65	0.209
15C......	" "	....	5.66	0.099	1.19	12.0	0.64	0.72	0.113
19A......	" "	19.0	5.80	0.429	5.01	11.7	0.48	0.82	0.235
19B......	" "	18.0	5.90	0.200	2.54	12.7	0.37	0.80	0.231
19C......	" "	....	5.97	0.088	1.16	13.2	0.37	1.04	0.141
24A......	Rhode Island bent pasture soil	18.0	6.61	0.447	5.00	11.2	1.80	0.76	0.339
24B......	" "	20.0	7.56	0.182	2.69	14.8	1.72	0.71	0.263
24C......	" "	....	8.21	0.045	0.60	13.3	1.77	0.95	0.205
25A......	" "	24.0	5.89	0.267	4.93	18.5	1.17	0.32	0.123
25B......	" "	23.0	5.80	0.181	4.80	26.5	1.33	0.19	0.118
25C......	" "	....	5.55	0.068	1.48	21.8	1.71	0.24	0.116
26A......	" "	22.0	5.97	0.273	3.96	14.5	0.91	0.64	0.183
26B......	" "	15.0	6.40	0.064	1.53	23.9	0.92	0.90	0.095
26C......	" "	....	6.41	0.046	0.54	11.7	1.11	0.91	0.133

TABLE IV. (Continued)

Sample No. and Horizon	Description	Depth of Horizon Centimeters	Soil Reaction pH	Total Nitrogen N%	Organic Carbon C%	Ratio Carbon Nitrogen	Total Calcium CaO %	Total Magnesium MgO %	Total Phosphorus P_2O_5%
Mean A..	Horizon "	....	5.88±0.09	0.335±0.017	4.91±0.11	15.2	0.98±0.11	0.59±0.05	0.188±0.012
Mean B..	" "	....	6.05±0.16	0.171±0.030	2.87±0.23	17.6	0.87±0.12	0.67±0.05	0.172±0.015
Mean C..	" "	....	6.04±0.29	0.078±0.007	1.24±0.17	15.4	1.01±0.13	0.72±0.07	0.129±0.009
7A......	Sweet vernal pasture soil	9.0	5.67	0.302	4.62	15.3	0.52	1.06	0.137
7B......	" "	16.0	5.61	0.237	3.10	13.1	0.56	0.97	0.149
7C......	" "	....	5.47	0.111	1.52	13.7	0.87	0.84	0.151
9A......	" "	11.0	5.77	0.389	5.36	13.8	0.42	0.85	0.175
9B......	" "	20.0	5.76	0.139	1.92	13.8	0.37	1.02	0.094
9C......	" "	....	5.28	0.082	1.08	13.2	1.19	1.13	0.087
12A......	" "	9.0	5.65	0.308	5.23	17.0	0.52	0.66	0.169
12B......	" "	27.0	5.65	0.190	2.89	15.2	0.27	0.75	0.114
12C......	" "	....	5.23	0.085	1.06	12.5	0.40	1.12	0.096
Mean A..	Horizon "	....	5.69±0.02	0.333±0.016	5.06±0.12	15.3	0.48±0.02	0.86±0.06	0.160±0.007
Mean B..	" "	....	5.67±0.020	0.188±0.016	2.63±0.20	14.0	0.40±0.05	0.91±0.05	0.119±0.009
Mean C..	" "	....	5.33±0.03	0.093±0.005	1.22±0.08	13.1	0.82±0.12	1.03±0.05	0.111±0.011
10A......	Poverty grass pasture soil	15.0	5.76	0.265	3.71	14.0	0.95	1.07	0.145
10B......	" "	17.0	5.80	0.121	1.29	10.7	0.51	0.37	0.088
10C......	" "	....	7.20	0.050	0.60	12.0	0.27	0.63	0.077
$16A_1$.....	" "	1.5	4.82	0.766	14.63	19.0	0.78	0.65	0.248
$16A_2$.....	" "	10.0	5.18	0.188	2.61	13.9	0.65	0.92	0.129
16B......	" "	18.5	5.01	0.244	4.99	20.4	0.15	0.62	0.180
16C......	" "	....	5.00	0.165	3.58	21.7	0.21	0.96	0.148
$17A_1$.....	" "	3.0	5.18	0.531	15.20	28.6	0.34	0.81	0.233
$17A_2$.....	" "	17.0	5.57	0.373	3.72	10.0	0.23	0.95	0.157
17B......	" "	20.0	5.05	0.115	2.42	21.0	0.12	0.61	0.139
17C......	" "	....	5.37	0.101	1.65	16.3	0.08	0.78	0.130
18A......	" "	10.0	5.05	0.547	14.40	26.3	0.14	0.44	0.218
18B......	" "	28.0	5.13	0.355	5.25	14.8	0.15	0.59	0.186
18C......	" "	....	5.15	0.166	3.02	18.2	0.18	0.85	0.153
22A......	" "	22.0	7.50	0.203	2.67	13.2	1.06	0.49	0.107

TABLE IV. *(Continued)*

Sample No. and Horizon	Description	Depth of Horizon Centimeters	Soil Reaction pH	Total Nitrogen N%	Organic Carbon C%	Ratio Carbon Nitrogen	Total Calcium CaO %	Total Magnesium MgO %	Total Phosphorus P_2O_5%
22B......	Poverty grass pasture soil	20.0	8.27	0.114	2.38	20.9	1.84	0.87	0.144
22C......	" "	....	8.60	0.056	1.22	21.8	7.87	2.84	0.168
23A......	" "	15.0	7.92	0.189	3.24	17.1	1.20	0.38	0.101
23B......	" "	17.0	7.90	0.142	2.85	20.1	1.54	1.13	0.088
23C......	" "	....	8.59	0.100	2.51	25.1	5.10	2.72	0.183
Mean A..	Horizon "	....	....	0.417±0.058	8.97±1.59	19.7	0.74±0.10	0.64±0.07	0.175±0.030
Mean A..	" "	....	....	0.280±0.044	3.16±0.26	23.9	0.44±0.10	0.93±0.01	0.193±0.017
Mean B..	" "	....	....	0.182±0.030	2.86±0.40	17.9	0.53±0.20	0.70±0.07	0.137±0.011
Mean C..	" "	....	....	0.106±0.013	2.00±0.29	19.2	2.28±0.85	1.46±0.26	0.143±0.010
27A......	Moss and fern pasture soil	14.0	4.74	0.264	4.62	17.5	0.23	0.46	0.251
27B......	" "	10.0	5.26	0.264	4.53	17.2	0.27	0.70	0.273
27C......	" "	....	5.26	0.109	1.72	15.8	0.58	1.01	0.165
$28A_1$.....	" "	3.0	5.12	0.911	15.49	17.0	0.71	0.42	0.263
$28A_2$.....	" "	3.0	5.15	0.635	10.32	16.3	0.47	0.21	0.225
28B......	" "	14.0	4.76	0.234	4.51	19.3	0.36	0.32	0.157
29A......	" "	18.0	4.85	0.179	3.47	19.4	0.14	0.30	0.128
29B......	" "	10.0	4.84	0.179	3.55	19.8	0.39	0.40	0.149
29C......	" "	....	5.00	0.085	1.46	17.2	1.01	0.81	0.078
$30A_1$.....	" "	3.0	5.75	1.489	22.54	15.1	0.44	0.44	0.284
$30A_2$.....	" "	12.0	5.37	0.206	7.21	35.0	0.51	0.63	0.261
30B......	" "	25.0	5.20	0.169	3.82	22.6	2.79	0.41	0.156
31A......	" "	15.0	5.06	0.421	2.42	5.8	0.43	0.50	0.116
31B......	" "	25.0	5.04	0.063	1.44	22.9	0.82	0.56	0.066
31C......	" "	....	5.50	0.045	0.60	13.3	0.15	0.73	0.069
32A......	" "	18.0	5.20	0.208	2.81	13.5	0.26	0.57	0.202
32B......	" "	22.0	5.18	0.131	1.87	14.3	0.18	0.41	0.192
Mean A_1.	Horizon "	....	5.12±0.09	0.579±0.13	9.56±2.14	14.7	0.37±0.05	0.45±0.02	0.207±0.018
Mean A_2.	" "	....	5.26±0.05	0.421±0.10	8.76±0.74	25.6	0.49±0.01	0.42±0.10	0.243±0.009
Mean B..	" "	....	5.05±0.05	0.173±0.018	3.29±0.33	19.3	0.80±0.25	0.47±0.03	0.164±0.017
Mean C..	" "	....	5.25±0.08	0.079±0.01	1.26±0.19	15.4	0.58±0.14	0.85±0.05	0.104±0.017

TABLE V. *Results of oxidation of aloin solution by soils.*

Sample number	Description	Increase of nitrates on storage	Percentage gain in color of aloin over original
1A	Blue grass pasture	High	81
5A	" " "	High	171
6A	" " "	High	245
14A	Rhode Island bent	Low	19
19A	" " "	High	217
16A	Poverty grass pasture	Low	41
17A	" " "	High	111
18A	" " "	Very low	26
27A	Moss and fern pasture	Very low	19
28A	" " " "	Very low	41
29A	" " " "	Low	26
30A	" " " "	High	100

TABLE VI. *Available phosphate in forest and pasture soils. Illinois rapid test.*

Sample No.	Description	Horizon A_1	Horizon A_2	Horizon B	Horizon C
4	Forest Soil	Low	Doubtful	Medium	....
8	” ”	High	....	Very high	Very high
11	” ”	Medium	....	Medium	Very high
20	” ”	High	....	High	Very high
21	” ”	High	Very high	Very high	High
33	” ”	High	....	Medium	Very high
1	Blue grass pasture	Medium	....	High	Very high
2	” ”	Medium	....	High	....
3	” ”	Doubtful	....	Medium	High
5	” ”	Doubtful	Medium	Very high	High
6	” ”	Medium	Doubtful	High	....
34	” ”	High	....	Very high	....
13	Rhode Island bent pasture	Doubtful	....	Doubtful	Medium
14	” ”	Medium	....	Medium	High
15	” ”	Doubtful	....	Medium	Medium
19	” ”	High	....	High	High
24	” ”	High	....	Very high	Very high
25	” ”	Low	....	Low	Medium
26	” ”	High	....	High	Very high
7	Sweet vernal pasture	Medium	....	Low	Doubtful
9	” ”	Medium	....	Low	Medium
12	” ”	Medium	....	Medium	High
10	Poverty grass pastuie	Medium	....	Medium	Very High
16	” ”	Medium	High	Low	....
17	” ”	Low	Doubtful	Medium	Low
18	” ”	Low	....	Low	Low
22	” ”	High	....	High	Very High
23	” ”	High	....	High	Very High
27	Moss and fern pasture	Medium	....	High	High
28	” ”	Low	Low	Doubtful	....
29	” ”	Medium	....	Medium	Medium
30	” ”	Low	Low	Low	....
31	” ”	Low	....	Doubtful	Medium
32	” ”	High	....	Very High	High

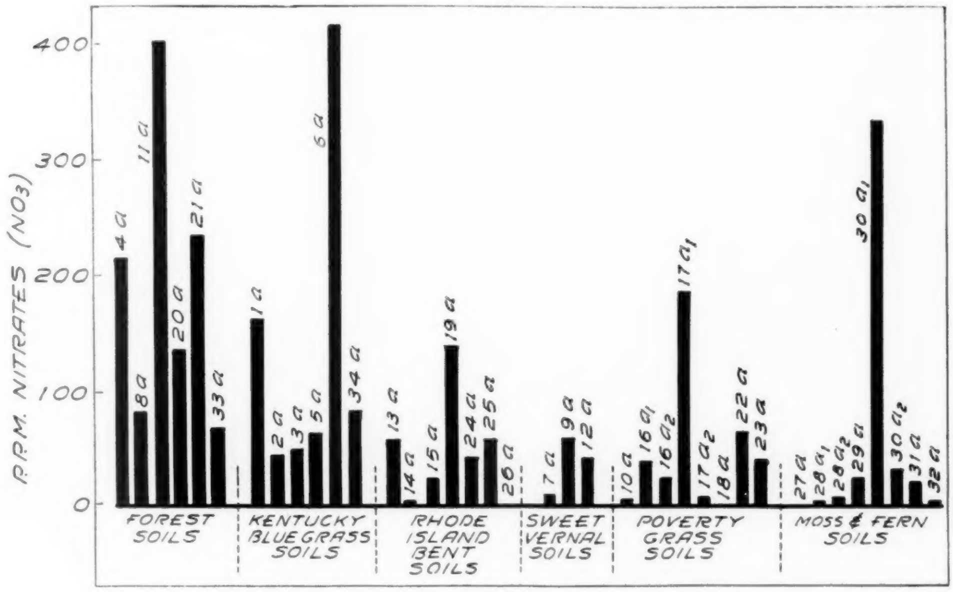

FIG. 1. Gain in nitrate nitrogen made by forest and pasture soils.

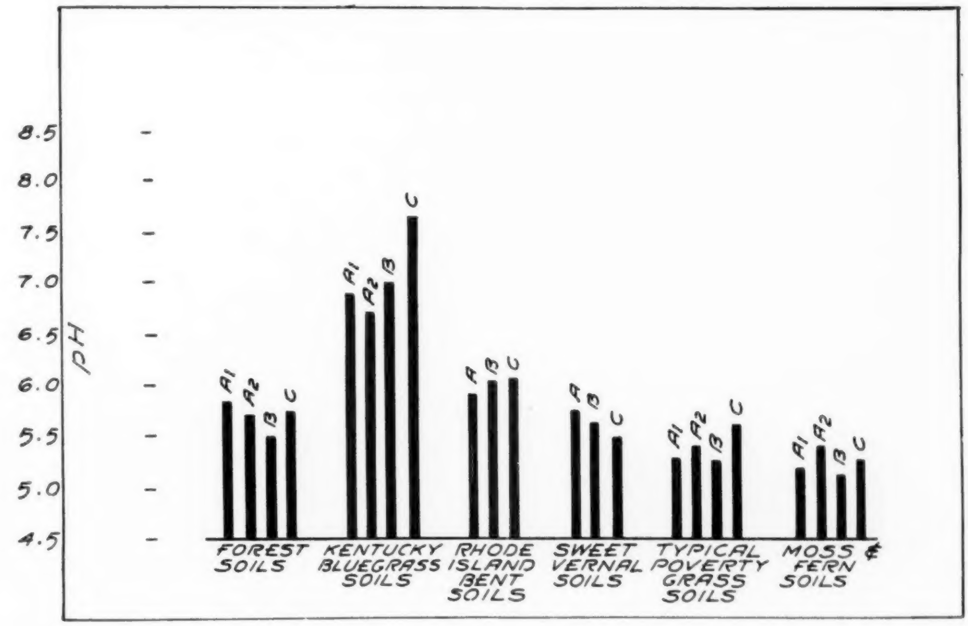

FIG. 2. Mean soil reactions (pH) of forest and pasture soils.

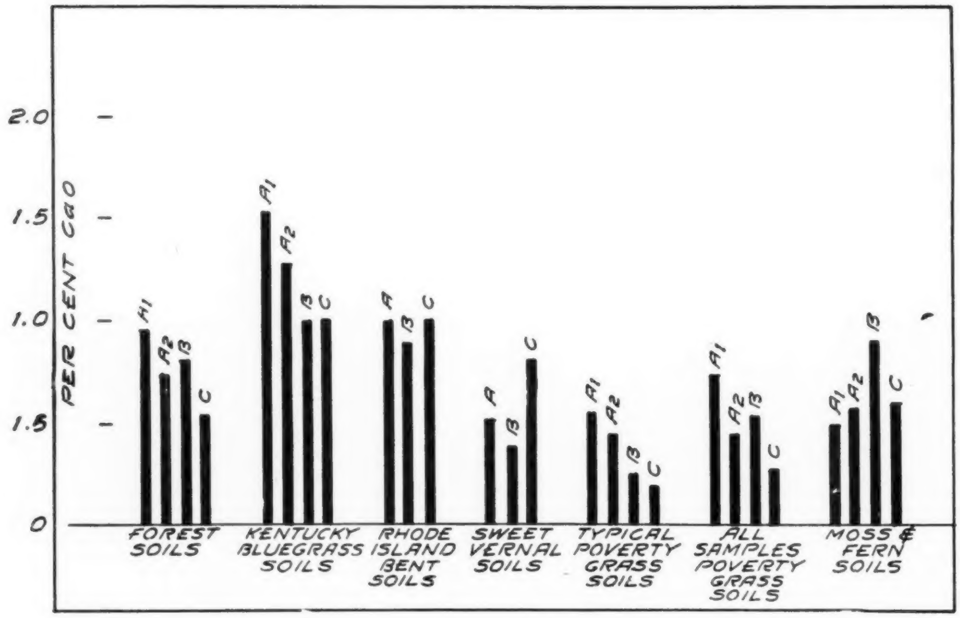

FIG. 3. Mean content of calcium (CaO) in forest and pasture soils.

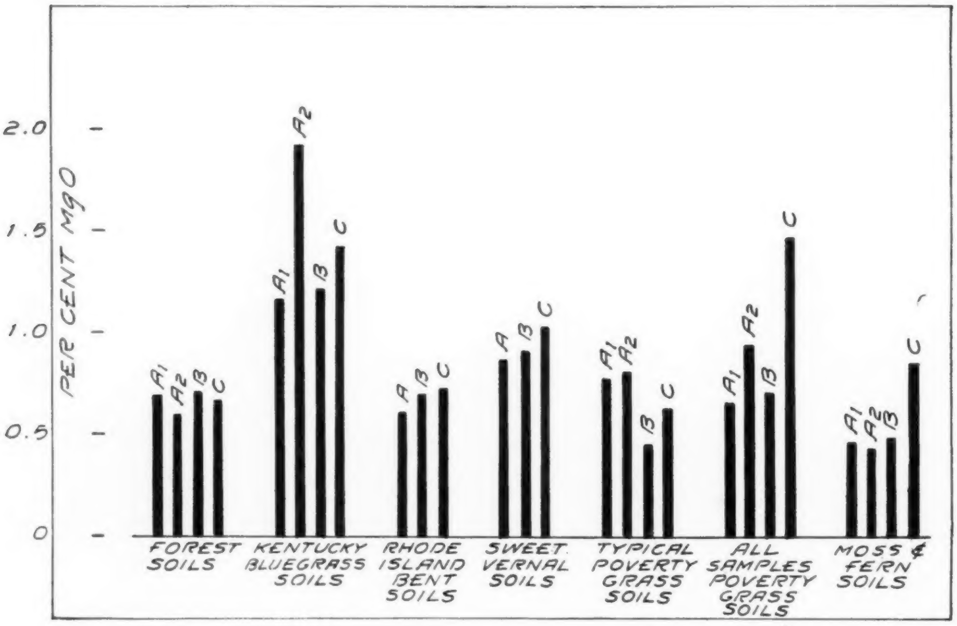

FIG. 4. Mean content of magnesium (MgO) in forest and pasture soils.

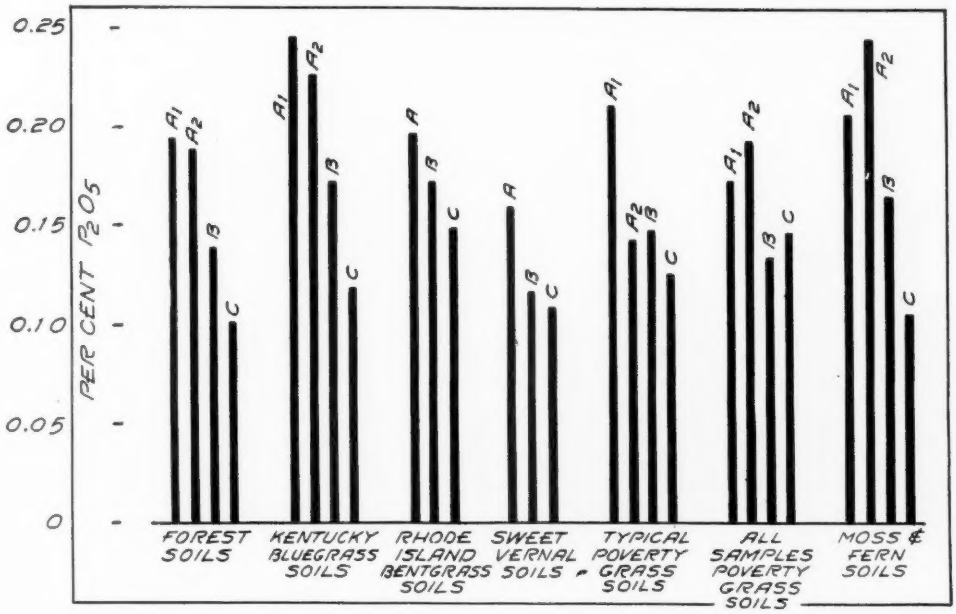

FIG. 5. Mean content of total phosphates (P_2O_5) in forest and pasture soils.